THE ECOLOGY OF THE GUM TREE SCALE (*ERIOCOCCUS CORIACEUS* MASK.), AND ITS NATURAL ENEMIES

BY

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CONTENTS

SUMMARY

The ecology of Eriococcus coriaceus Mask., an indigenous Australian scale insect found on gum trees, was studied in the grounds of the Waite Agricultural Research Institute.

Sixteen species of natural enemies belonging to the orders Neuroptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera were found attacking the scale. The scale were also attended by ants and in the experimental area these were a small species of Iridomyrmex.

The history of the outbreak of E. coriaceus, which was introduced into New Zealand, and its control by the coccinellid Rhizobius ventralis is discussed. Initial observations on the scale are outlined.

The scale had four generations a year with major periods of reproduction at the end of winter (August) and late spring (November). Females of the summer and autumn generations produced young from January to April, chiefly in January and March. The length of the female is closely related to her fecundity and to the number of embryos she contains. There was a seasonal cycle in female size, smaller females being produced in summer and especially in early autumn. The sex ratio of the young also varied, a greater proportion of female young being produced in spring than in late summer. Other aspects of the biology, such as the settling of the crawlers, colony formation by the females and wing forms in the males are also examined.

Populations of the scale were studied in the field. Sampling methods are outlined. The adult females were most abundant in the cooler months, August and November, the population of female scale declining from

November to January. This decline coincides with heavy predation by *R. ventralis*. Populations were apparently kept at a low level in summer (when *R. ventralis* was absent) because of parasitism by two species of *Aphycopsis* (Hymenoptera:Encyrtidae), other natural enemies including larvae of the moths *Catoblemma* spp. (Noctuidae) and by the low fecundity of the female scale.

Attendance by *Iridomyrmex* sp. caused an increase in the rate of excretion of honeydew by nymphs of *E. coriaceus*. It did not influence the rate of development, survival or fecundity of the scale in the laboratory. The protection these ants give the scale in the field was examined. Ten large and ten small populations of scale were established in the field; half were attended by ants and ants were excluded from half. Ant attendance increased the percentage survival of the female scale in both large and small populations, a higher percentage of female scale surviving in large populations than in small ones. In large attended populations there was a substantial reduction in the percentage of scale killed by *R. ventralis*; how scale in small attended populations were protected is not known. The numbers of ants attending the scale were related to the number of scale; there was no evidence that small populations of scale were relatively better attended by ants (and therefore better protected) than large ones. *R. ventralis* is able to co-exist with the ants because the larvae emerge at night, when there are few ants, to feed. Ant attack on the larvae of *R. ventralis* is described; the ants reduce the numbers of larvae of *R. ventralis* and *Chrysopa ramburi* feeding on *E. coriaceus* on small trees. Nymphs produced by the female scale on eight trees in the experiment described above survived when attended by ants but all unattended populations were wiped out by R. ventralis. Ant attendance at night was examined and for the ants attending one scale population attendance was found to vary with temperature. Examination of several scale populations on summer nights showed they were well attended by ants. It seems likely therefore that the rarity of R. ventralis in summer is due, at least in part, to the continuous attendance of ants.

The biology of the natural enemies of the scale is examined. Particular attention is paid to R. ventralis and its life history, rate of development, its feeding and oviposition preferences for female scale of different sizes, and seasonal abundance. The disappearance of this coccinellid during the hot summer months is discussed. Adults aggregated on trees with large numbers of scale but despite this a greater percentage of female scale were killed in small populations than in large ones. The adaptations of the natural enemies to a life with ants are discussed, those best adapted to living with ants occurring during the summer when ants are numerous and those most poorly adapted occurring during the winter when ants are scarce.

The influence of crowding on various population processes is examined. When very large populations of females occur on a tree dense colonies may be formed and the females in these contain fewer embryos than in less dense colonies. Many of the active stages produced in such populations walk off the tree. On small trees this leads to a relatively constant number of females settling. As the number of female scale on a tree increases their size (and hence fecundity) decreases, and the sex ratio of the young they produce, although variable, changes from being mainly female to being mainly male. The influence of population density on tree growth is also examined.

The conclusion is drawn that outbreaks of *E. coriaceus* do not occur in Australia because of the efficiency and wide powers of dispersal of their natural enemies. The main reason that populations exist which can persist for several years on one tree is the presence of the attendant ants which prevent *R. ventralis* from completely destroying the scale.

Declaration

The work presented in this thesis is my own unless otherwise acknowledged, and has not previously been published or submitted to any university for the award of any degree.

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(Neil Gough)

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CHAPTER 1 INTRODUCTION

1.1 Introduction

Eriococcus coriaceus, the Gum Tree Scale, is indigenous to Australia where it attacks *Eucalyptus* spp. in Queensland, New South Wales, Victoria, South Australia and Tasmania (Hoy, 1963). It was first described by Maskell (1893) from material from Sydney.

E. coriaceus is interesting because it is the centre of a small but complex ecosystem. It is preyed on by a large number of natural enemies exhibiting a great diversity of habits. It is also attended by ants whose presence modifies the action of some of the natural enemies. Another notable aspect of the scale is that, although it never reaches large numbers in Australia, it has been introduced into New Zealand, where it was at one time a pest of some importance.

1.2 Historical information

In Australia few accounts of *E. coriaceus* have been published. Froggatt (1907, 1921) was an astute naturalist and described some of the most important features of the biology of the scale which he found commonly in the eastern states (Queensland, New South Wales and Victoria) in localized populations. Although he observed considerable numbers of scale on some trees he noted that he had never seen "even a sapling" killed, and concluded that the populations were kept at a low level by a host of natural enemies. He observed that the scale occurred most abundantly in October and November (mid and late spring).

Patel (1971) worked on *E. coriaceus* at the Waite Institute, where this study was also conducted. He examined the morphology of the male and the immature stages and made important observations on the biology of the scale. Although he produced a list of the predators and parasites he gave no indication of their relative importance, times of occurrence, or biology. Other authors simply mention the scale (Tillyard 1926) or refer to it as infesting eucalypts grown in gardens.

In 1900 *E. coriaceus* appeared at Timaru, in the South Island of New Zealand, where it became a serious pest of the *Eucalyptus* forests which had been established there, attacking particularly *E. globulus* and *E. stuartiana* which were important timber trees. Kirk (1908) reviewed the history of the outbreak and its subsequent decline. He thought that the scale had been introduced either on young gum trees or more probably on hardwood logs used for wharf pilings. Within a year all plantations within a 16 km radius of Timaru were infested. Soon large trees, 20-25 m high, succumbed and large areas of plantations were beginning to die. In less than 5 years, an area over 290 km in length was infested. At this time there were 22,000 ha. of eucalypts (valued at that time at over £1 million sterling) in the South Island alone.

Kirk introduced three species of coccinellids, *Rhizobius ventralis*, *Cryptolaemus montrouzieri* and *Orcus chalybeus*. All were originally from Australia, but the stock for some of his releases came from the North Island where the beetles had been introduced previously. They were reared in outdoor breeding stations, but only *Rhizobius ventralis* survived the cold winter. Kirk distributed this species widely throughout the infested area and in three years the scale ceased to be a major problem in the area where the scale was first abundant. Kirk describes the control of the scale thus:

"Since the initial distribution of Rhizobius the work accomplished by this insect has been little short of marvellous, and through its means Eriococcus has been relegated to a position of insignificance in the gum-plantations of the South. In all parts of the affected area the scale is being rapidly eaten out, and around Timaru, the original centre of infection, it has entirely disappeared. The rapidity with which Rhizobius has multiplied is almost incredible. In January of this year my assistant collected at Rolleston over 1,300 on ten gum trees in a little over three hours, so that the numbers in a large plantation are almost beyond the conception of the imagination. In Australia the balance of power is even between the ladybird and the blight, and both blight and ladybird are always present; but in New Zealand, the ladybird being, as it were, in pure cultures and unhindered by the presence of any secondary parasites, is much more powerful than the scale, and completely wipes it out. It is not too much to say that within another twelve months there will scarcely be a single living scale to be found on the southern plantations, which only three years ago were swarming with the pest and to all appearances doomed to utter destruction".

The scale was probably dispersed by the wind and in 1921 it crossed over Cook Straight and appeared on a wide front in the North Island. The spread over the North Island also followed the prevailing winds and by 1938 the scale had spread over most of New Zealand (Miller and Clark, 1935; Clark, 1938). Whenever it reached a new area it caused considerable damage but was then usually swiftly overtaken by R. ventralis and in 1938 Clark considered that the scale could no longer be regarded as a major pest.

Since that time the population of the scale has been kept at a low level by *R. ventralis*, which is found in most colonies of the scale (Zondag, 1974 pers. comm.). The moth *Stathmopoda melanochra*, and the fly *Pseudoleucopis beneficia* were introduced later (Miller and Clark, 1935) but only the former became established. It now seems of little importance in reducing populations of the scale (Zondag, pers. comm.).

The initial destruction of vast numbers of *E. coriaceus* by *R. ventralis* and the subsequent suppression of the scale population must rank as one of the classical examples of biological control, and it is somewhat puzzling that it has remained so obscure, there being few references to it in the general ecological literature (Miller, 1918; Sweetman 1958; DeBach 1964). Perhaps it was because Kirk introduced the coccinellids at an early stage and was so successful that the forestry industry was never threatened.

1.3 The study area

The ecology of the scale was studied in the grounds of the Waite Agricultural Research Institute. Two study areas were used. Firstly, near Alverstoke Orchard where 50 eucalypts (5 species, 10 trees of each species) had been planted in 1969 and were about 2 m high when the work began in August 1971. These trees were planted in two rows with about 1.2 m between the rows and a similar distance between the trees within the rows. The other area used was the block of Mallee

TABLE 1.1 Climatological summaries (temperature and rainfall) for Waite Agricultural Research Institute, 1925-1973.

Month	Average daily air temperature °C			Rainfall (mm)
	Max.	Min.	Mean*	
January	27.8	16.2	22.0	23.0
February	27.4	16.3	21.8	27.5
March	25.6	15.4	20.5	20.6
April	21.5	12.9	17.2	57.0
May	17.7	10.5	14.1	81.5
June	15.1	8.5	11.8	74.9
July	14.1	7.7	10.9	84.9
August	15.1	7.9	11.5	74.1
September	17.6	9.2	13.4	60.5
October	20.3	10.8	15.5	51.7
November	23.2	12.6	17.9	39.5
December	25.7	14.5	20.1	31.0
				626.2

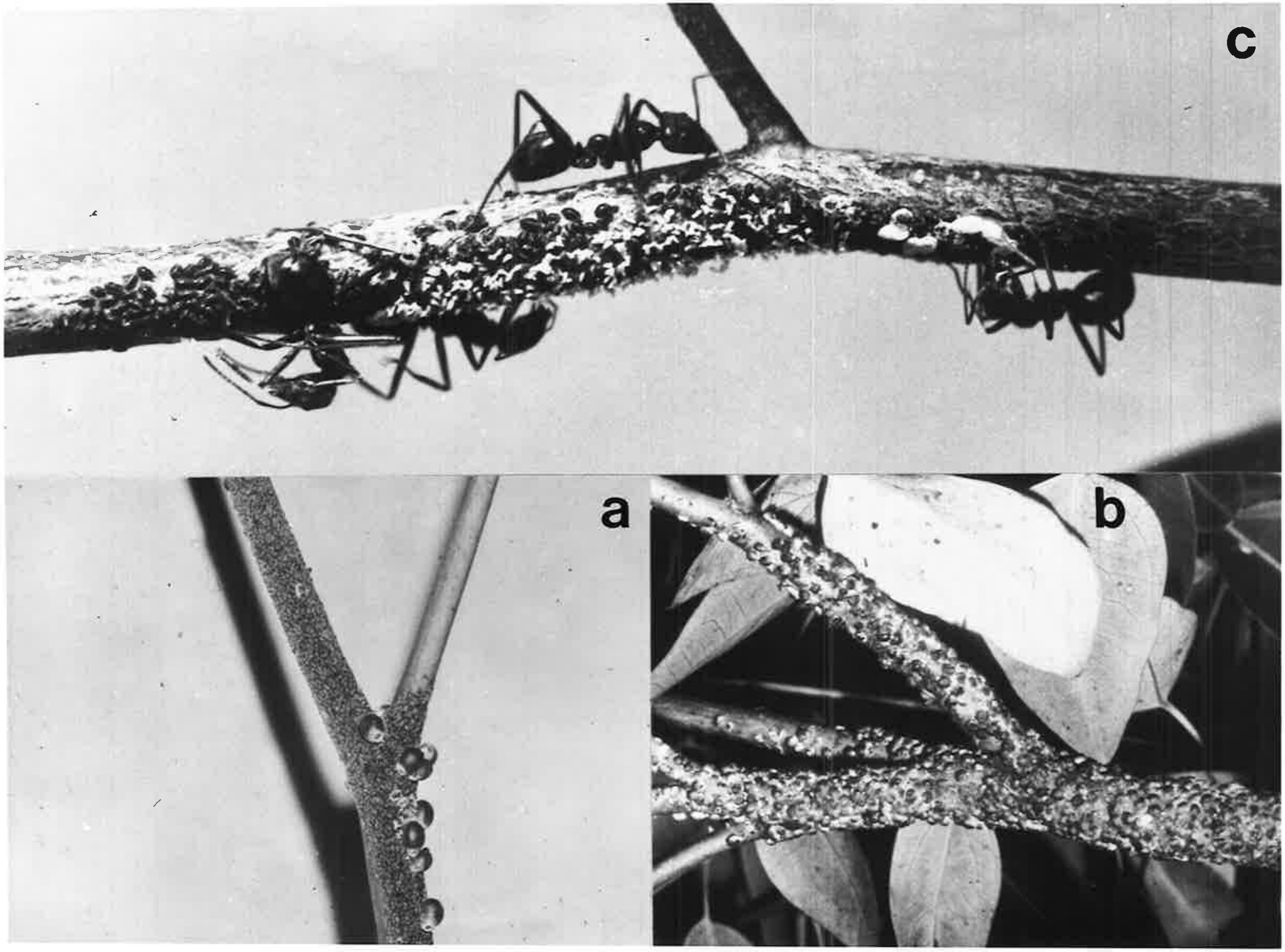
$$* = \frac{\text{max.} + \text{min.}}{2}$$

Figure 1.1

1.1(a) Female *E. coriaceus* surrounded by a dense colony of newly settled first instar nymphs (Approx. x 2)

1.1(b) A colony of female *E. coriaceus* (Approx. x 1)

1.1(c) Ants (*Iridomyrmex purpureus*) attending newly moulted second instar nymphs. Note the cast exuviae which are white (Approx. x 4.5)


c
a
b

trees (Eucalyptus spp.) near the Waite Arboretum which contains some 300-350 trees.

Various species of tree were used, because there were no extensive stands of one species, and these with the code numbers I use are referred to in appendix Table 1.

Gums occur throughout the grounds of the Waite Institute and in the hills to the east. These support populations of the scale and its predators. Thus the system which was examined was by no means isolated and was similar in many ways to situations in which scale occur naturally in the wild.

1.4 The climate of Adelaide

As there are marked seasonal trends in some of the properties of E. coriaceus, and in the composition of the predator complex, the climate is briefly discussed.

The average daily maximum, minimum and mean temperatures and rainfall recorded at the Waite Institute for the years 1925-1973 are given in Table 1.1. (Biennial Report of the Waite Agricultural Research Institute, 1972-1973).

Although there are slight differences in the weather of the Waite Institute and the Bureau of Meteorology in Adelaide the following comments on the climate of Adelaide (South Australian Year Book, 1974) apply in broad terms also to the Waite Institute.

In the summer months, maximum temperatures are high and frequently exceed 30°C. Occasionally heatwaves with temperatures near or over

Figure 1.2

Colonies of female *E. coriaceus*.

38°C are experienced for several consecutive days. July is the coldest month with a mean maximum of 15°C, August is only slightly warmer than July but, after August, steadily rising temperatures are experienced during the spring months.

Adelaide is the driest of Australia's capital cities. The summer rainfall is light and unreliable, the average monthly precipitation from January to March being less than 25 mm. Completely rainless months in this time are not uncommon. Each month from May to September averages over 50 mm and in this period the rainfall is fairly reliable. June is the wettest month but the average for this month is still less than 75 mm. The 134 year rainfall average for Adelaide is 527 mm.

1.5 A brief description of the biology of *E. coriaceus*.

This brief description is given to provide the reader with background information. The points outlined below are treated in detail in later chapters.

The female scale is sessile (Figure 1.1(a)), apart from a short period after her final moult, when she wanders in search of a feeding site. Her body is initially almost flat but soon after settling it begins to increase in size; her ovaries develop, expanding greatly and eventually taking up most of the body cavity. Immediately before she reproduces, which may be from about 1 to 4 months after she has settled, a female may contain up to 400 or more well developed embryos.

Soon after the female settles in the feeding site she begins to secrete a test which covers her body almost entirely (except for a caudal opening) after about a week. The body of the female (and the test) increases in size as her ovaries develop; the test is consolidated by continued secretions and may be eventually quite tough. The body of the scale fills the test completely. The crawlers emerge through the caudal opening in the test. The test is usually orange brown in colour although at times it may be stained black by a sooty mould which grows on honeydew. The length of the female scale (including the test) varies greatly but at reproduction is most commonly between about 2.5 and 3.25 mm. The scale are ellipsoidal (at times almost spherical) being about three quarters as broad as they are long and slightly less high. I use the term "scale" to mean the actual body of the coccid and also the enclosing test. If the coccid dies or is destroyed by predators the test remains attached to the tree and usually bears marks left by, and characteristic of, the predator or parasite.

The female scale settle in aggregations, which I call "colonies", usually on the twigs of the tree (Figure 1.1(b), 1.2). Even when there are few (e.g. 100 or so) scale on a tree colonies are usually still formed. The females settle in a regular manner forming colonies of fairly uniform density. In autumn the young females sometimes may settle on the leaves often forming small aggregations.

There were four generations a year in the study area. Reproduction occurred in late winter, usually August, the females of the succeeding generations producing young in November, January and early February, March and early April. Reproduction was often well synchronized within a population on a tree and, except in late summer, fairly well synchronized between populations on different trees within the area studied.

Once reproduction begins young are produced quickly and in large numbers. In laboratory studies female scale died soon after giving birth. The young also form very dense, well delineated colonies (Figure 1.1(a)).

E. coriaceus has a life history typical of the coccids. The females pass through two moults before settling as adults. They move actively over the tree as crawlers and after the first and second moults. The males have an extra moult, entering a pupal stage after the second nymphal instar and emerging as winged adults (illustrated in Chapter 2).

During the course of the study some 16 species of predators and parasites were reared from the scale. Chief among these were *Chrysopa ramburi* (Neuroptera - Chrysopidae), *Rhizobius ventralis* (Coleoptera - Coccinellidae), *Pseudoleucopis beneficia* (Diptera - Chamaemyiidae), *Catoblemma dubia*, *C. mesotaenia* and *Stathmopoda melanochra* (Lepidoptera - Noctuidae and Stathmopodidae), *Aphycopsis* spp. (Hymenoptera - Encyrtidae).

The scale were attended by ants, in the area near the Waite Institute a small species of *Iridomyrmex*. Figure 1.1(c) shows *I. purpureus* attending newly moulted second instar nymphs.

Notes: The sexes of the first instar nymphs can not be easily distinguished and scale early in the first instar are usually referred to as "crawlers". For convenience "females" or "female scale" are used to refer to the adult female scale; where female second instar nymphs are referred to this is explicitly stated.

I use "population" to refer to the scale on one tree. This is a realistic definition for although the mobile stages wandered widely over the trees up to 4 m high (and presumably over even larger ones) they did not disperse so readily between trees. This was obvious because heavily infested trees were frequently surrounded by uninfested trees only 1-2 m away.

1.6 Initial observations

1.6A First generations observed

To begin observations on *E. coriaceus* I chose three trees in the plantation near Alverstoke Orchard infested with the scale. The trees were sugar gums (*E. cladocalyx*) and were designated Obs. 1, 2 and 3. At this time only adult females were present and these were counted and examined on the trees to determine the number of living scale and the causes of death. These females began to produce large numbers of young about 20th August. Few predators were seen; these were larvae and adults of the coccinellid *Rhizobius ventralis* and the larvae of *Chrysopa ramburi*. Some nymphs were killed by predators and some were probably washed away by rain but overall the survival rate of the nymphs appeared to be high.

At this time (August and September 1971) I could not estimate how many young were produced (and subsequently died) because of sampling difficulties. However, when the adult females began to settle it was apparent that, even though two populations increased greatly, it would be possible to estimate the numbers of female scale (methods for estimating the number of female scale on a tree are explained in Chapter 3).

The females of the next generation began to settle in October. The populations of females that settled in October on Obs. 1, 2 and 3 respectively were 78.0, 53.4 and 16.6 times greater than the populations in the previous generation. The population of female scale on one tree examined in the Mallee Block (1842A) also increased markedly (13.9 times) over the number of females present in August.

1.6B The measurement of causes of mortality to the female scale and of the lengths of the survivors

It was apparent that some estimate of the proportion of females surviving to reproduce, and the causes of mortality, could be obtained. Furthermore, Patel (1971) had shown that the length of the female when she reproduced was related to the number of young she produced. My own data (2.3A) confirmed his work and I began measuring the length of females to estimate fecundity.

The development of methods for estimating mortality to the female scale are outlined, for data from these early samplings (August and November 1971) are used later (3.4).

The females have a long preoviposition period after they have settled and during this time they are exposed to the natural enemies. The predators and parasites usually killed the scale in characteristic ways so that even if the body of the coccid was destroyed the test (which remained on the tree) bore evidence of the cause of death.

(This matter is discussed in more detail in Chapter 5).

In August 1971 all the females in each population were examined, *in situ*, to determine the causes of mortality. As the populations increased, such observations were impossible in the next generation and a sample was therefore examined from the population on each tree.

When a female first settles in the final feeding site it is naked and very delicate and can not be marked. However, once the test has been secreted an individual may be easily marked with a spot of white plastic paint.

To determine the proportion of scale killed between settling and the completion of the test, areas of newly settled females were delineated using entomological steels driven into the twigs. The enclosed areas were photographed from the same angle every two days until the females began to secrete their tests. Colour transparencies were made and by comparing transparencies taken on successive days it was possible to identify individual scale. The number which had died or disappeared could then be determined. The cause of death of some females which had secreted a large part of their test could also be determined by examining the condition of the test. Few females died between the time they settled and the time they had secreted sufficient test to show where they had been and usually to identify what killed them. The photographic method was therefore not used again and I relied on finding the tests of the dead females to show how many had settled and what had killed them.

When the newly settled females had secreted sufficient of their tests, 50 were chosen in the populations on Obs. 1 and Obs. 2 with as little bias as possible and each was marked with a spot of white paint. These were examined before and during reproduction and the extent and causes of mortality determined.

Soon after the females had begun to reproduce the marked scale were removed from the trees and dissected to determine which were alive. An equal number of females which were apparently alive were chosen to replace survivors in the sample dissected. These were also dissected at a later date when the production of crawlers had almost ceased. Before both groups of scale were dissected their lengths were measured (to the nearest .015 mm) and the number of embryos they contained counted.

Female scale usually had to be removed from the tree so that their lengths could be accurately determined, and to be dissected to see if they contained parasites. Removing individuals proved difficult because they were usually located in colonies and the removal of a single scale often entailed the destruction of a large area of scale about it.

The causes of death of the scale on tree 1842A (in the Mallee Block) was thus determined in a different way, and five areas of scale, chosen with as little bias as possible, each containing about 50 individuals, were removed. The bark sliver bearing the scale was removed with a scalpel. The females were dissected and the causes of death noted. From each sliver the lengths of a sample of the surviving females were measured. If there were more than 10, they were numbered, and 10 were chosen at random and their lengths were measured.

This method of removing bark slivers was used from January 1972 onwards. Five or ten samples were taken from a population by choosing colonies at random from the number determined during the sampling to estimate the total population of female scale (see 3.1). These chosen colonies were tagged and when reproduction began, an area in each was chosen without bias by tossing a coin.

The estimates of mortality in 3.4 and elsewhere throughout the study were obtained by adding the number of scale destroyed by each predator in all of the samples taken at one time from a population and expressing this as a percentage of the total number of scale examined in those samples. The number of female scale examined from each population to determine the causes of mortality is shown in Table 2 (appendix).

1.6C Reproduction by the female scale. November 1971

Reproduction in November was similar to that in the previous generation in August in that large numbers of crawlers were produced quickly and settled over extensive areas of the tree. No females survived to reproduce on Obs. 3 and reproduction was not carefully followed on tree 1842A in the Mallee Block. Comments are therefore restricted to populations on trees Obs. 1 and 2.

The rate of recruitment of young to the population was not measured directly at this time, but some estimate of the rate of reproduction was obtained by examining the females. It was demonstrated (2.3A) that the number of embryos a female scale contains immediately before reproduction is closely related both to her length and to the number of young she is capable of producing.

Note. When I refer to the length of the female scale I mean in fact the length of the test. As the female scale fills the test completely and the test itself is very thin (see Figure 5.1(a)) this is a close approximation to the actual body length of the coccid. The length of the scale does not alter appreciably after reproduction for although the actual body of the coccid may shrivel, as the ovaries are emptied, the test remains the same size. This was demonstrated by measuring the length of 20 scale before and after reproduction; there was no significant difference in the lengths at the two times. This was convenient, for at times it allowed me to estimate the number of young a female produced even when she had completed reproduction.

On the 19th November, about one week after crawlers first appeared, surviving females (among those which had been marked) were removed from the trees, their lengths measured and the number of embryos they contained counted. The number of embryos they would have contained immediately before reproduction was estimated from their lengths, using the equation below, which is derived in 2.3A.

$$y = 305.87x - 550.10$$

where y is the number of embryos contained by females x mm long.

The actual number of embryos the females contained on 19th November (about one week after the beginning of reproduction) was less than half that which I estimated they had originally contained.

<u>Number of embryos.</u>

	Before reproduction	After 7 days	As % of total
Obs. 1	419*	198	47.3
Obs. 2	306*	117	38.2

* estimated

Further dissections three weeks after reproduction began showed that the bodies of the females contained mainly fluid and a few well developed embryos (less than 10% of the estimated total). Reproduction in these populations was therefore well synchronized and quickly completed. Similar findings are reported for another population in July and August 1973 where the actual number of young settling on the tree was measured (Chapter 2.3B).

1.6D The estimation of the number of crawlers produced in the second generation, November and December 1971.

From the populations where there were surviving females which were closely observed (Obs. 1 and 2) large numbers of crawlers were produced. As females of *E. coriaceus* lay eggs which (in warm weather) hatch in about 10 minutes (Patel, 1971), it is not possible to determine directly the number of nymphs entering the first instar. The only way of estimating the number of young produced is to calculate the number of surviving females, estimate their fecundity from their mean length and then multiply the two together. As reproduction was well synchronized in these populations the survival rates of the females about one week after large numbers of young appeared were used to estimate the numbers of females surviving and reproducing from estimates of the total populations of females. The numbers of young produced by the females on Obs. 1 and Obs. 2 may be calculated as follows:

	Obs. 1	Obs. 2
Population of female scale (see 3.2)	14,905	30,174
Percentage survival of females at time of reproduction	64%	26%
Number of females reproducing	9,539	7,845
Mean length of individual female scale	3.17mm	2.80mm
Number of young produced per female *	485.3	370.9
Total number of crawlers produced	4,630,000	2,910,000

* calculated from the equation relating female size (x) and fecundity (y) derived in 2.3A : $y = 309.16x - 494.74$

1.6E The estimation of the number of nymphs on the tree

After the nymphs leave the ovisac of the female scale they may wander over the surface of the tree for up to 6 hours before they settle (Patel, 1971). When they settle on the tree they form very dense colonies. The mean density was estimated at 669 first instar crawlers per square centimeter (2.3B). The total population of young on the tree may be determined by measuring the total area the colonies covered and multiplying by the mean density. The area was measured as described later (3.1) by using a pair of vernier calipers.

On both trees nymphs of the scale had been destroyed by adult and larval coccinellids and chrysopid larvae. The areas destroyed could be measured because ragged patches of the scale remained and the areas once occupied by nymphs (which had been eaten) were frequently stained with the reddish body fluid of the scale. The area covered by the live

TABLE 1.2(a) Estimated number of young produced by females on tree Obs. 1. The subsequent decline in numbers until the settling of adult females.

	Area covered by nymphs	Estimated no. of nymphs	% of total produced	% of those females that settled
Total offspring produced		4,630,000	100.0	
Total ♀ offspring produced*		2,940,000		
Total first instars settled December 3rd	727.0 cm^2	486,000	10.5(1)	
♀ first instars settled December 3rd*	462.0 cm^2	309,000		100.0
Total live first instars December 3rd	686.0 cm^2			
Live ♀ first instars December 3rd*	436.0 cm^2			94.4(2)
Total live nymphs December 10th (many second instars)	536.0 cm^2			
Live ♀ nymphs December 10th*	341.0 cm^2			73.8(2)
Number of adult females which settled		21,600	.467(1),(3)	6.97(1)

* 63.6% of young trapped from this tree were females (6.1C). Total areas and estimated numbers have been multiplied by .636 to determine areas and numbers of females.

1. Percentages based on estimated numbers.
2. Percentages based on areas covered.
3. 21,600 is .467% of the total young produced and .734% of the total ♀ young produced.

NOTE: Although rounded figures are shown in the tables the original data has been used for calculations.

TABLE 1.2(b) Estimated number of young produced by females on tree Obs. 2. The subsequent decline in numbers until the settling of adult females.

	Area covered by nymphs	Estimated no. of nymphs	% of total produced	% of those females that settled
Total offspring produced		2,910,000	100.0	
Total ♀ offspring produced*		745,000		
Total first instars settled December 3rd	815.0 cm^2	545,000	18.7(1)	
♀ first instars settled December 3rd*	209.0 cm^2	140,000		100.0
Total live first instars December 3rd	287.0 cm^2			
Live ♀ first instars December 3rd*	73.0 cm^2			35.2(2)
Total live nymphs December 10th (many second instars)	86.0 cm^2			
Live ♀ nymphs December 10th	22.0 cm^2			10.6(2)
Number of adult females which settled		1,100	.037(1),(3)	.78(1)

See footnotes to previous table.

* 25.6% of young trapped from this tree were females.

(1), (2) As before

(3) 1,100 is .037% of the total young produced and .146% of total ♀ young produced.

nymphs on December 3rd was measured. The total area which had originally been covered could be estimated by measuring the patches where the nymphs had been and adding these areas to the areas covered by the live nymphs. By 10th December many of the nymphs had moulted and colonies of second instar nymphs were formed.

1.6F Causes of mortality to the nymphal stages

Tables 1.2(a) and 1.2(b) show the estimated number of young produced by the females and the estimated number of first instar nymphs that settled. In the estimate for 3rd December I assumed the density of the nymphs was 669 per square centimeter. By the time many of the crawlers had moulted for the first time (10th December) the assumption that the density was 669 per square centimeter was not justified for obviously, as the nymphs increase in size, the number per square centimeter decreases. Thus areas covered, as well as estimated numbers, are used in Tables 1.2(a) and 1.2(b). Any sampling plan to follow trends in numbers of immature *E. coriaceus* using the areas covered would also have to include a continuous assessment of density.

The most obvious feature of the data is that many of the young which I estimated to have been produced were not present in the population on 3rd December. It seems likely that the possible reproductive potential of the female scale is not always realized in the field, but the discrepancy is too great to be accounted for entirely in this way. Only 10.5% of the total young expected on Obs. 1 and 18.7% on Obs. 2 had settled. Vast numbers of crawlers walked off the trees, especially Obs. 1, and I believe this explains most of the loss. Attempts were not made to trap the nymphs because the traps would have interfered with the ants which were ascending the stem and tending the scale. (Later experiments showed the attendance of ants to have an important influence on the survival of the scale). This massive loss of nymphs is discussed elsewhere (6.1A).

There were different trends in the survival of the nymphs that settled on the two trees. The areas of nymphs on Obs. 1 and Obs. 2 on December 10th were 73.7% and 10.6% respectively of the areas covered by nymphs which initially settled on those trees. The numbers of individuals alive at this time were obviously less than 73.8% and 10.6% of those that settled on the trees, for the density on 10th December was much less than that on 3rd December. The difference in survival rates was accounted for by the different numbers of predators that were present on the two trees.

The predators present were Rhizobius ventralis and Chrysopa ramburi. The numbers of chrysopid larvae and adult coccinellids were small on both trees. A survey of six large branches with scale on each tree on 6th December showed that there were no significant differences in the numbers of these predators on the two trees. There was, however, a significant difference in the number of larvae of R. ventralis ($p < .01$, Mann Whitney U Test).

In addition to the coccinellid larvae on the branches there were at least 35 others under the bark on Obs. 2 whereas on Obs. 1 there were only about 3 or 4 in a knothole on the stem and several under a

Total number of predators on six branches (infested with scale) on the two trees. (6th December 1971).

	Obs. 1	Obs. 2
Chrysopid larvae	1	2
R. ventralis adults	0	0
R. ventralis larvae	0	16

small piece of loose bark. The reason for these differences was not discovered but was almost certainly tied up with the attendance of ants and led to an examination of the relationship between the ants and the scale. This is described in Chapter 4.

Predation continued on both populations between 10th December and the final settling which took place in late December. A survey on 31st December showed that predators were then more common on Obs. 1 than on Obs. 2, a reversal of the former situation probably resulting from the very low population of scale that remained on Obs. 2 after the initial heavy attack by predators.

The total number of predators on six branches (infested with scale) on the two trees. December 31st, 1971.

	Obs. 1	Obs. 2
Chrysopid larvae	6	1
R. ventralis adults	8	3
R. ventralis larvae	0	0

Adult *R. ventralis* (but no larvae) were seen in late December and in early January these disappeared. No eggs or larvae of *R. ventralis* were seen in the female scale dissected in late January and none of the scale examined bore the typical marks caused by predation by coccinellids. This decline in the population of coccinellids was very surprising because of the large population of scale on two of the survey trees at this time. (Obs. 1: 21,600 female scale; Obs. 4: 10,100 female scale). Chrysopid eggs and larvae also became very uncommon whereas mortality caused by hymenoptera and stathmopodid moths increased.

The mortality to the immature stages in both populations was very great, for 6.97% and .78% of the females present on 3rd December settled as adults in late December on trees Obs. 1 and Obs. 2 respectively.

Whilst it was obvious that predators, particularly the larvae of R. ventralis played an important part in reducing the population on Obs. 2 the reason for the decline on Obs. 1 was more difficult to understand. Predators were not so numerous on this tree and on the surveys on 3rd and 10th December (Table 1.3(a)) relatively small areas of scale had been destroyed. As I have already observed, very large numbers of crawlers left Obs. 1 and this trend continued for newly moulted and mobile second instar and adult females also walked off the tree. Although predation continued on this population (see table above for 31st December) the predators probably had fairly little impact because there were no R. ventralis larvae and the C. ramburi larvae were very small in size (probably second instars).

Thus the reduction in population on Obs. 2 could be attributed to nymphs walking off the tree but more importantly to heavy predation by coccinellid larvae. Predators were fewer on Obs. 1 and I believe the great reduction in population on this tree was caused by the majority of the nymphs walking off the tree.

1.7 Conclusions from the initial observations and general plan of the study

1. Despite careful and prolonged attempts at sampling, the errors in estimating the numbers of the immature stages were likely to be very great and only a rough picture of the causes and extent of mortality to the nymphs could be obtained. This conclusion was reinforced by the complexity of the processes operating in the population on Obs. 1 in January 1972. In this large population (21,600 scale) females formed very dense colonies in which their fecundity was reduced by crowding (6.1D). Although no measurements were made it seems likely that the sex ratio of the young produced by these females probably changed from being predominantly female to being predominantly male (6.1C). Once again, many nymphs walked off the tree. Even the estimation of the number of nymphs which remained on the tree in late January would have been extremely difficult. In November, although large numbers of nymphs were produced, they were confined to relatively few large colonies (41 colonies on Obs. 1 and 73 on Obs. 2). In January, however, much of the available surface area of the tree had been occupied by the previous generation whose tests remained on the tree (see 2.2B). This forced the crawlers produced by females in January to form a large number of smaller colonies on the outer ends of the twigs and these were extremely difficult to sample.

I had originally intended to try to construct life tables for successive generations and to determine the factor, or factors, causing the major variations in population trends. Southwood (1966) discusses these methods very fully. This was clearly impossible for I was working on my own and the sampling problems were insurmountable.

2. The natural enemies obviously played an important part in the ecology of the scale. The population on Obs. 3 (764 females) was completely extinguished by *C. ramburi* and *R. ventralis*; the population on Obs. 2 declined from 30,200 females in November to 1,100 in January, largely through the influence of predators. Most of the females examined from the population on 1842A in the Mallee Block in November 1971 had been killed by predators.

There were also marked changes in the species of natural enemies attacking *E. coriaceus*. *R. ventralis* and *C. ramburi* were present from September until December but by January the coccinellids had disappeared and the chrysopids were in very small numbers. Hymenopterous parasites, which had not been common previously, attacked many of the scale. (Refer to 3.4 for quantitative estimates of the mortality discussed above).

3. Despite the ability of the predators to destroy large numbers of scale their action was more irregular than I expected. The above fairly well documented observations showed that the population on Obs. 1 increased from 14,900 females to 21,600 females in the next generation, despite the presence of a large number of predators which caused the collapse of populations on two trees not 3 m distant. There was no question of the predators not finding this population as adult coccinellids

were seen on the tree but few coccinellid larvae were produced.

4. It seemed that density dependent negative feedback mechanisms came into operation when the number of scale settling on a tree was very large. Thus in November 1971 the scale on Obs. 1 were significantly larger than those on Obs. 2 (populations 14,900 and 30,200 respectively). The reverse occurred in January for then the population on Obs. 1 was greater than that on Obs. 2. (See 6.1B). Other evidence from these early observations is presented in 6.1.

With these points in mind the study of *E. coriaceus*, its natural enemies and attendant ants developed in the following way:-

I decided to outline the ecology of the scale by a relatively long term study, sampling only the adult female stage to determine numbers, causes of mortality and approximate fecundity. The methods and results are outlined in Chapter 3.

In Chapter 2 aspects of the biology of *E. coriaceus* are discussed. Some of the information used in this chapter comes from the survey discussed in Chapter 3 but I think the rationale behind the sampling plan and methods in Chapter 3 is much easier to understand if the biology of the scale is discussed first.

Many ants began attending the scale in the late spring and summer of 1971 and 1972. I knew that ants could protect Homoptera from their natural enemies (Way, 1963) and thought that some differential protection by the ants might provide an answer to the irregular action of the predators. The relationship between *E. coriaceus* and ants (*Iridomyrmex* sp. B in particular) was therefore examined experimentally (Chapter 4).

During the course of these investigations, information accumulated on the biology of some of the natural enemies of _E. coriaceus_, and these, with other observations, are presented in Chapter 5.

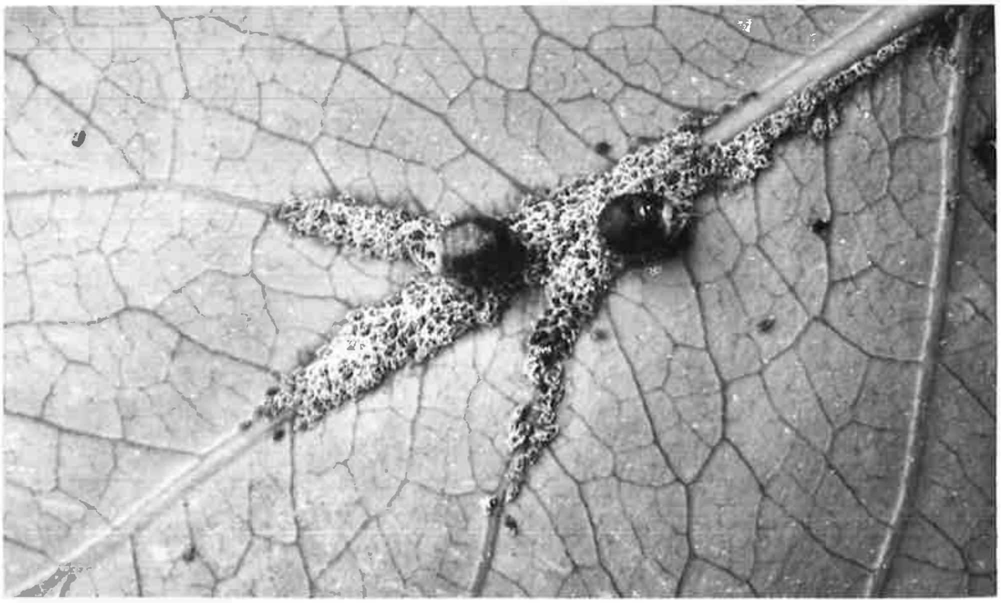
Evidence of the effect of crowding accumulated from the survey and from simple experiments. In September 1973 I started an experiment in the Kuitpo Forest Reserve to examine the influence of crowding on both the quality of the female scale and the rate of growth of the tree. Both the preliminary observations and this experiment are discussed in Chapter 6.

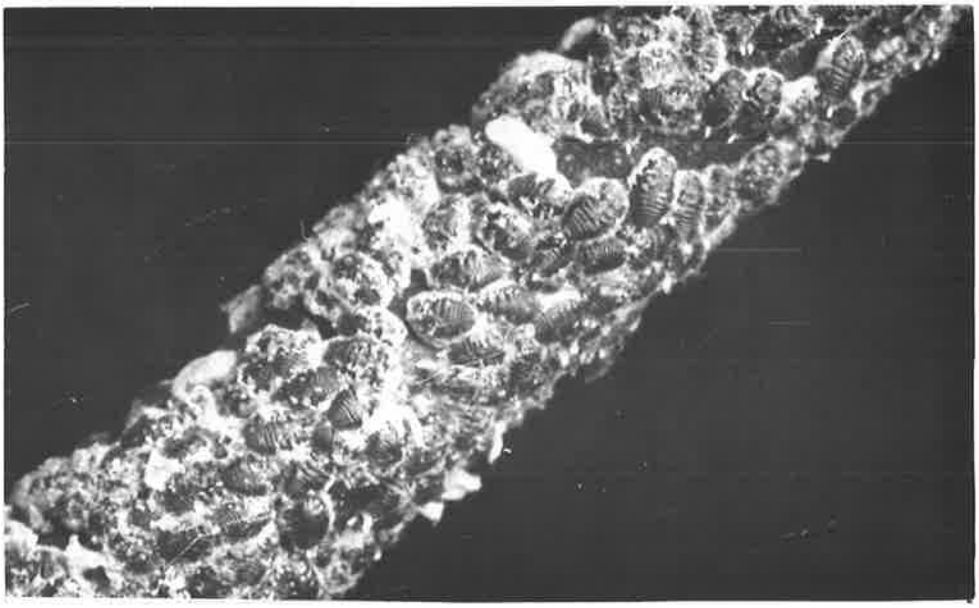
Chapter 7 contains a general discussion.

Figure 2.1

(a) Reproducing female E. coriaceus with first instar nymphs settled nearby (approx. x 4.5)

(b) A colony of newly settled second instar nymphs.





CHAPTER 2

Aspects of the biology of *E. coriaceus*

2.1 Biology of the immature stages

Patel (1971) described the immature stages and the adult male of *E. coriaceus*. He also described the general biology of the insect. The female scale passes through two moults from crawler to adult. The male passes through an extra moult, entering a pupal stage and finally emerging as a winged adult. The following is a brief abstract of Patel's account (Patel's work is acknowledged) with some new observations.

2.1A The nymphal stages

The females are oviparous but the egg stage lasts only about 10 minutes in warm weather (Patel 1971). Eggs are laid in the ovisac formed between the body of the female and her test. After oviposition the shrivelled white chorions may be found in the ovisac. The first instar nymphs remain in the ovisac quiescent for about 12 hours after they hatch before finally leaving through the caudal opening (Patel).

There are three periods of great mobility in the life of the female scale. She may move actively and search for a feeding site as a crawler, and after the first and second moults.

Patel states that the crawlers wander for up to six hours before settling on a tree. Crawlers tend to settle near their mothers (Figure 2.1(a)) but in dense populations they are often forced to move further afield where they form new colonies. Under adverse conditions first instar nymphs may cease feeding, withdraw their stylets and move to another feeding site. The crawlers are highly thigmotactic so that they form colonies where individuals are packed as tightly as possible, the first instar nymphs often being found at densities of about 650 per square centimeter, and female second instars at densities of about 100 - 150 per square centimeter.

All stages except the first instar nymphs secrete a sac which remains on the twig when the insect moults. A white waxy secretion covers the dorsal surface but is simply cast with the nymphal skin giving the triangular white exuvia characteristic of the first moult (see Figure 1.1(c)). The sexes can not be distinguished in the first instar. At the end of the first instar the overall length of the nymph is about .71 mm (range .66 - .79 mm) whereas the newly emerged second instar nymphs are about .87 mm (range .83 - .90 mm).

After the first moult both sexes settle and begin feeding (Figure 2.1(b)). Within 2-3 days at 20°C differences in the form of the tests become apparent. The females secrete a felted sac, which is pink or orange. The male prepupa secretes a white cottony test under which it moults and pupates (see Figure 2.10(a)). Male and female second instar nymphs may be interspersed but also often form separate groups with the females centrally placed and the males around the periphery. This is especially common on leaves where the females settle near the midrib and the males further out on the blade of the leaf. When the population density is very high many thousands of male pupae may form aggregations on the less favourable parts of the tree such as the base of the stem (see Figure 2.10(b)). When there is a large population of scale much of the surface area of the tree may be occupied and males may thus avoid competing with the more actively feeding stages for the limited space at preferred feeding sites.

Colonies of nymphs are usually formed on the under surface of twigs.

At 20°C (± .5°C) the first instar nymphs completed development in 10.4 days (range 9-12 days) and the second instar in 13.7 days (range 12-15 days). In July and August 1973 when the maxima were generally about 15°C first instar nymphs took at least 21 days to develop and second instar females about a month.

2.1B The influence of the density of nymphs on their rate of settling

White (1970) found that the greater the number of nymphs of the psyllid *Cardiaspina densitexta* placed on aleaf disc the lower the percentage that had settled after 24 hours. Willard (1973) also showed that high densities retarded settling by crawlers of the red scale *Aonidiella aurantii*. It seemed likely that nymphs of *E. coriaceus* might settle more quickly at higher densities for, unlike the former two species, they form dense colonies. The settling behaviour was examined in the laboratory.

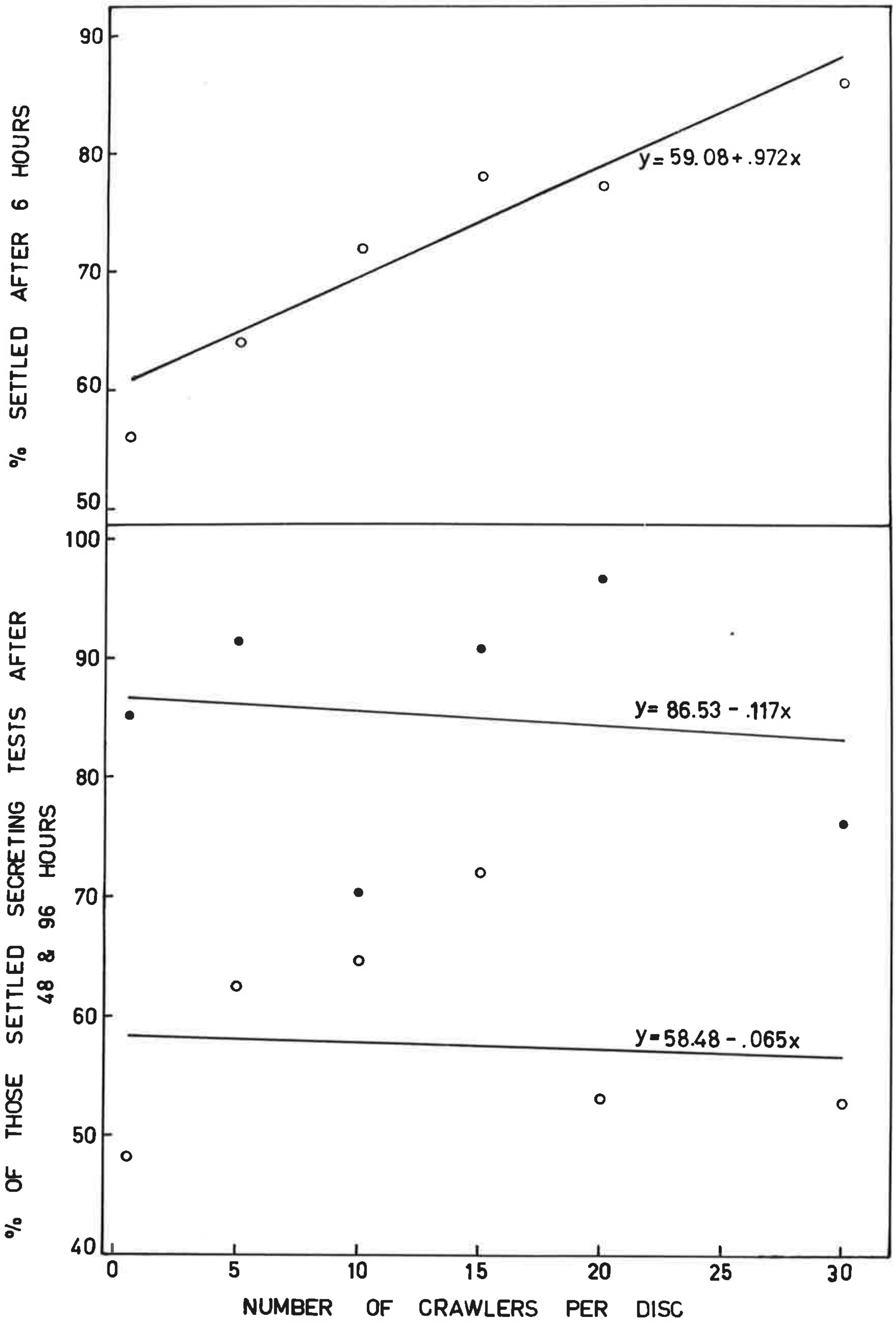
A similar method to that of White's was used except that the leaf discs were not subjected to inadequate light before the experiment began. Mature, healthy leaves were collected from the north face of a *E. cladocalyx* immediately before the experiment. A disc, 2 cm in diameter, including a central portion of midrib, was cut from each leaf and floated on distilled water in a small plastic vial (2.5 cm diameter and 5.4 cm high). The experiment was carried out in a glasshouse where the temperature varied between 19 and 24°C during the experimental period.

Figure 2.2

The influence of different densities on the settling and establishment rates of crawlers of *E. coriaceus*.

(a) Percentage of crawlers seeded that settled on the discs after six hours.

(b) Percentage of those that settled beginning to secrete wax after 48 hours (open circles) and 96 hours (closed circles).


% SETTLED AFTER 6 HOURS
90
80
70
60
50
y= 59.08+.972x
% OF THOSE SETTLED SECRETING TESTS AFTER 48 & 96 HOURS
100
90
80
70
60
50
40
y= 86.53 - .117x
y=58.48 - .065x
0
5
10
15
20
25
30
NUMBER OF CRAWLERS PER DISC

Sunlight was excluded and light was provided by two 400 W mercury vapour lights. Artificial light was necessary because seeding took more than four hours (8.30 a.m. to 1 p.m.) and the six hour period (see below) ran from 2.30 p.m. until 7.00 p.m., which was after nightfall.

First instar crawlers were transferred from a potted E. cladocalyx onto the discs with a fine brush. Six densities of crawlers were used (1, 5, 10, 15 and 30 per disc). The numbers that settled were counted six hours after the initial seeding. As it was impossible to see the early secretion of the test I assumed that the larvae had settled when their antennae and legs had been folded out of sight. After 48 and 96 hours the numbers of nymphs settled on the discs and the numbers secreting wax were counted.

Figure 2.2(a)(Table 3(a) appendix) shows the percentage of the total scale seeded in the different treatments which had settled after 6 hours. Analysis of the data (percentages not transformed) indicates that there is a highly significant regression of the proportion of nymphs that settled on the density of the crawlers (number per disc) ($F_{1,4} = 40.48$, $p < .005$). A greater proportion of crawlers drowned at lower densities especially on the treatment where they were placed singly on the discs (Table 3(a) appendix). This is a measure of their greater restlessness when confined alone on a leaf disc, for the further they wander the greater their chances of being trapped in the water. When one individual settled others soon followed and settled nearby so that the foreparts of their bodies touched that of the original colonizer. This behaviour created colonies which were very dense centrally but had many interstices around the edges (where the hind parts of those already established were not touching); new arrivals forced themselves into these spaces. Sometimes one large colony was formed but usually the larvae settled in a series of smaller colonies.

By contrast, the initial density of crawlers per leaf disc had no influence on the proportion of nymphs (expressed as a percentage of the number of nymphs settled at these times) surviving 48 and 96 hours after seeding (Figure 2.2(b); data in Table 3(b) appendix). The secretion of wax was the clearest indication that the nymphs were alive and feeding i.e. surviving. It was thus apparent that although larvae settled more readily at higher densities, the density of the colony formed did not influence the survival of the young.

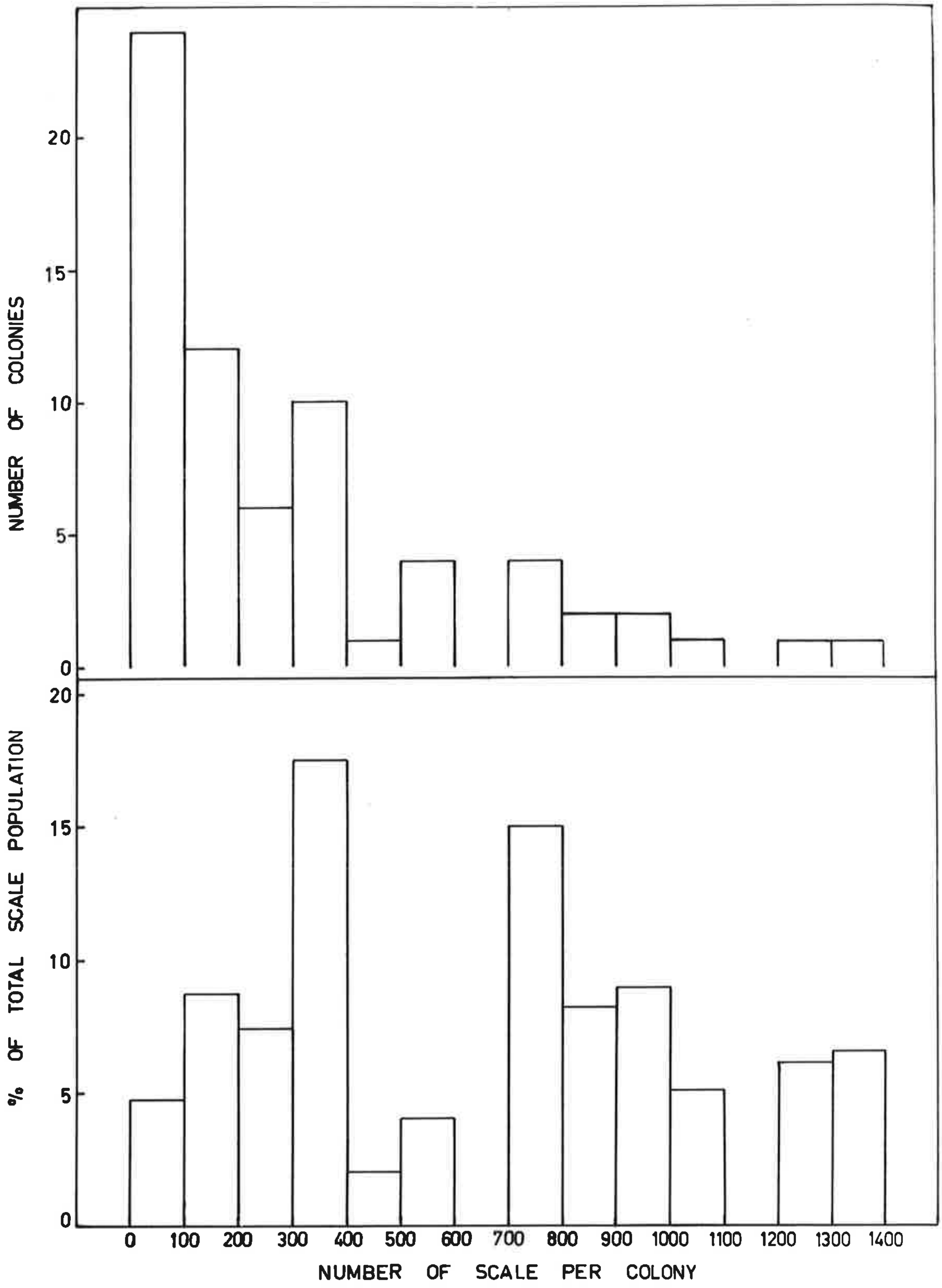
These findings differ from those of White (1970) who found that increasing the numbers of nymphs of _C. densitexta_ on leaf discs reduced the settling rate. He found that, after four days, there was evidence that more nymphs secreted tests or lerps at an initial density of 10 per leaf than at higher or lower densities.

One reason for the formation of very dense colonies of nymphs on trees may be that they collectively condition the area on which they feed and form physiological sinks, which compete with growing parts of the plants for nutrients and thereby greatly increase the chances of survival of the young. Way and Cammell (1970) showed that aggregations of aphids conditioned leaves of cabbage in the same way. (This question is briefly discussed elsewhere in relation to the formation of colonies of female _E. coriaceus_). It is surprising that the proportion of tests

Figure 2.3

(a) A typical sampling distribution of colony size for a population of female *E. coriaceus*

(b) The percentage of the total scale population contained in different sized colonies (same population as above).



NUMBER OF COLONIES
0
5
10
15
20
% OF TOTAL SCALE POPULATION
0
5
10
15
20
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
NUMBER OF SCALE PER COLONY

secreted by E. coriaceus nymphs does not increase with the increasing number of young settling on the leaf disc. It may be that although an advantage may be obtained by dense colonies on living trees, no advantage could be gained on excised portions of a leaf.

2.2 The adult female

2.2A The adult female settling patterns

The newly moulted females move widely over the tree and settle in distinct colonies where they begin to secrete their final tests soon after settling. The females almost invariably settle with their caudal openings pointing downwards (and so do not become contaminated with their own honeydew).

A typical sampling distribution of colony sizes is shown in Figure 2.3(a); Figure 2.3(b) shows the percentage of the total scale population on the tree contained in the different sized colonies. (Data from tree 1842A, Mallee Block, December 1971). The greatest number of colonies (20 out of 68) occurred in the smallest size class (0-100) but they contained less than 5% of the total scale population on the tree. On the other hand, 11 colonies each contained more than 700 scale and together these contributed half (49.3%) of the total scale population. Such patterns where the majority of individuals were found in a (relatively) minor proportion of the total number of colonies were common.

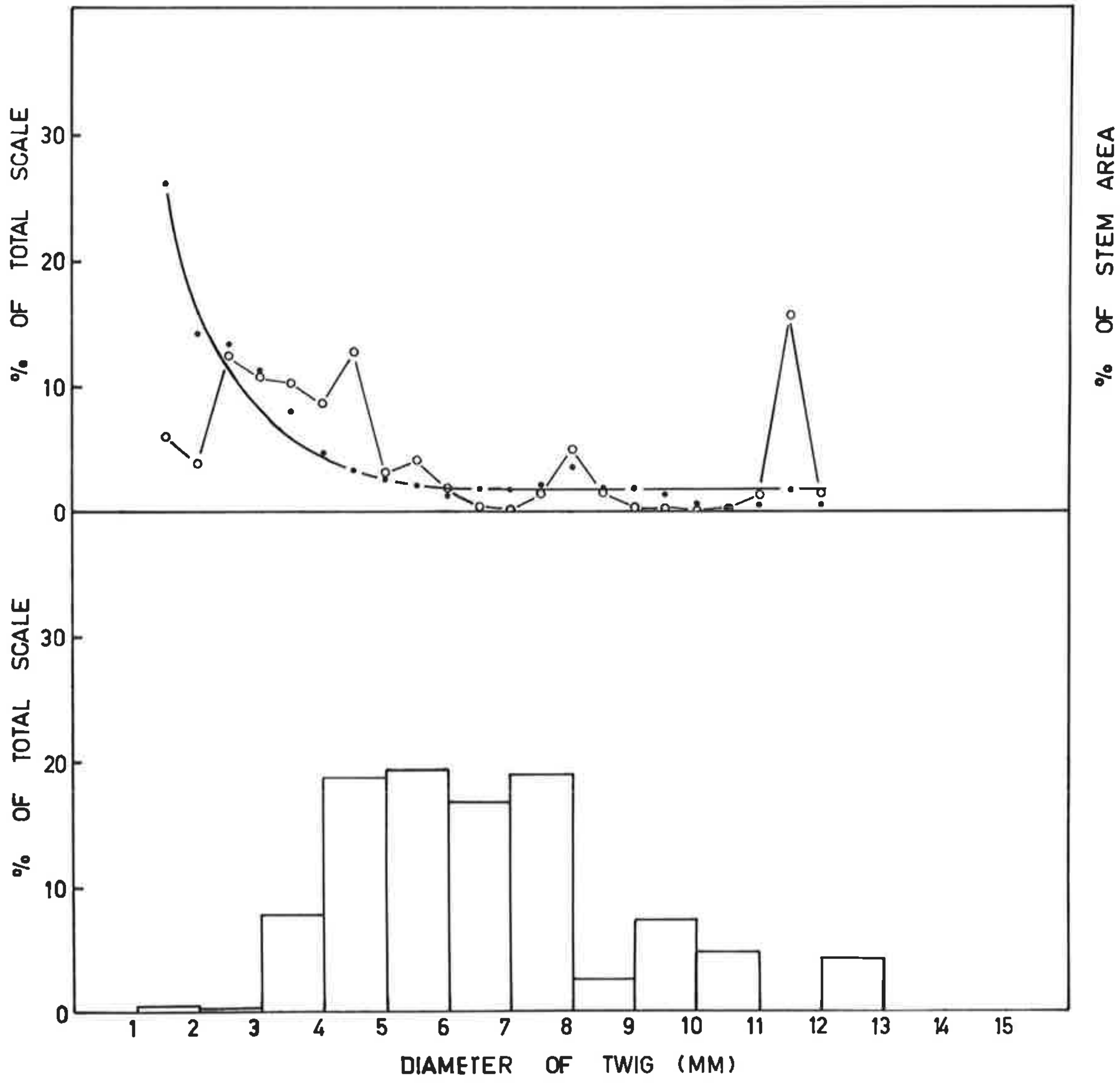
2.2B The distribution of the colonies on the twigs

Initial examinations of trees indicated that the colonies of scale were not distributed at random with respect to the diameter of the twigs available. The new growth and older thicker stems usually seemed to

Figure 2.4

(a) A comparison of the frequency distribution of the areas (at different diameters) available for settling and the areas (at different diameters) actually colonized.

(b) The relationship between diameter of twig and the percentage of the total scale population occurring at those diameters. The frequency distribution of surface area of twigs available would be similar to that in figure above.


% OF TOTAL SCALE
30
20
10
0
% OF STEM AREA
% OF TOTAL SCALE
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
DIAMETER OF TWIG (MM)

be avoided unless there was extreme over-crowding. To quantify the distribution of scale four large branches were chosen at random on one infested tree in July 1971. The contribution (expressed as a percentage of the total surface area) of twigs in different diameter classes was determined. This gave a frequency distribution of the areas available for settling, which can be compared with the areas actually colonized (Figure 2.4(a)). The two distributions were dissimilar ($\chi^2 = 60.0$; 6d.f.; $p < .001$. All data from 4.5 to 12.0 mm combined to give an expected value greater than 5. Bailey, 1959). Because of the small sample size the distribution of scale was somewhat erratic but there is an obvious accumulation of scale on twigs with diameters 3 to 6 mm; a similar accumulation of scale on twigs of 4 to 8 mm was also apparent on the population on the tree (1842A) previously mentioned (Figure 2.4(b)). The sampling distribution of the surface area contributed by twigs of different diameters would be similar to that of the previous tree sampled.

The whole of the surface area of the tree may not, however, be available for colonization by the scale, for the tests of the dead females stay on the tree for several months (and in some cases much longer), and the accumulative remains of several previous generations may thus prevent living scale from colonizing large areas of the tree. For example, on one tree (Obs. 1) on which several large successive generations of scale were produced, the surface area of all twigs above .25 cm was measured in November 1971 and the percentage of this area covered by female scale in each ensuing generation was estimated (see below). The females which covered 950 cm^2 in November 1971 died by January 1972 and excluded the next generation from colonizing an area of 950 cm^2 of the most favourable part of the tree. Females of the January generation likewise covered 24.6% of the total surface area of the tree. Thus when the females which reproduced in March began to settle, over half the area of the tree was already occupied by the tests of dead females.

Areas of tree Obs. 1 covered by female scale in succeeding generations

Sampling date	Area covered by females	% of total area of tree covered by scale	Cumulative % of total area of tree covered by scale
November 1971	950 cm^2	26.0	26.0
January 1972	806 cm^2	24.6	50.6
March 1972	606 cm^2	18.5	69.1

These figures are based on the assumption that the surface area of the tree did not increase between November and March. The rate of growth of the tree was much less than that of nearby trees of the same species and this was almost certainly because of the large scale population it was supporting (see 6.2Bc).

In addition, colonies of female nymphs also covered large areas of the tree. Thus in December alone 727 cm^2 (or 22.5% of the surface area) was covered by nymphs. Even taking into account a great deal of tree growth by March 1972, over 80% of the surface area of this tree had been utilized by the scale. Consequently the females were forced to form colonies on the outermost twigs with diameters less than those

TABLE 2.1 The influence of the length of the leaf on the percentage of leaves infested with female *E. coriaceus* and the mean number of scale per infested leaf.

Leaf size (cm)	No. leaves examined	% infested	Mean no. scale per infested leaf
2.0 - 2.9	10	0	0
3.0 - 3.9	55	12.7	1.9
4.0 - 4.9	131	30.5	5.5
5.0 - 5.9	69	68.1	8.9
6.0 - 6.9	42	81.0	9.8
7.0 - 7.9	18	72.7	37.9
8.0 - 8.9	14	92.9	20.2
9.0 - 9.9	7	85.7	35.3

normally preferred. The density of the colonies formed increased to such an extent that intraspecific competition had a marked influence on the rate of reproduction (see 6.1D).

2.2C Settling on the leaves

The adult female scale do not colonize only the twigs of the tree but they may also settle on the leaves, especially in autumn or when much of the surface area of the twigs has been covered by a large scale population. On some mallee trees the flower buds are also regularly infested.

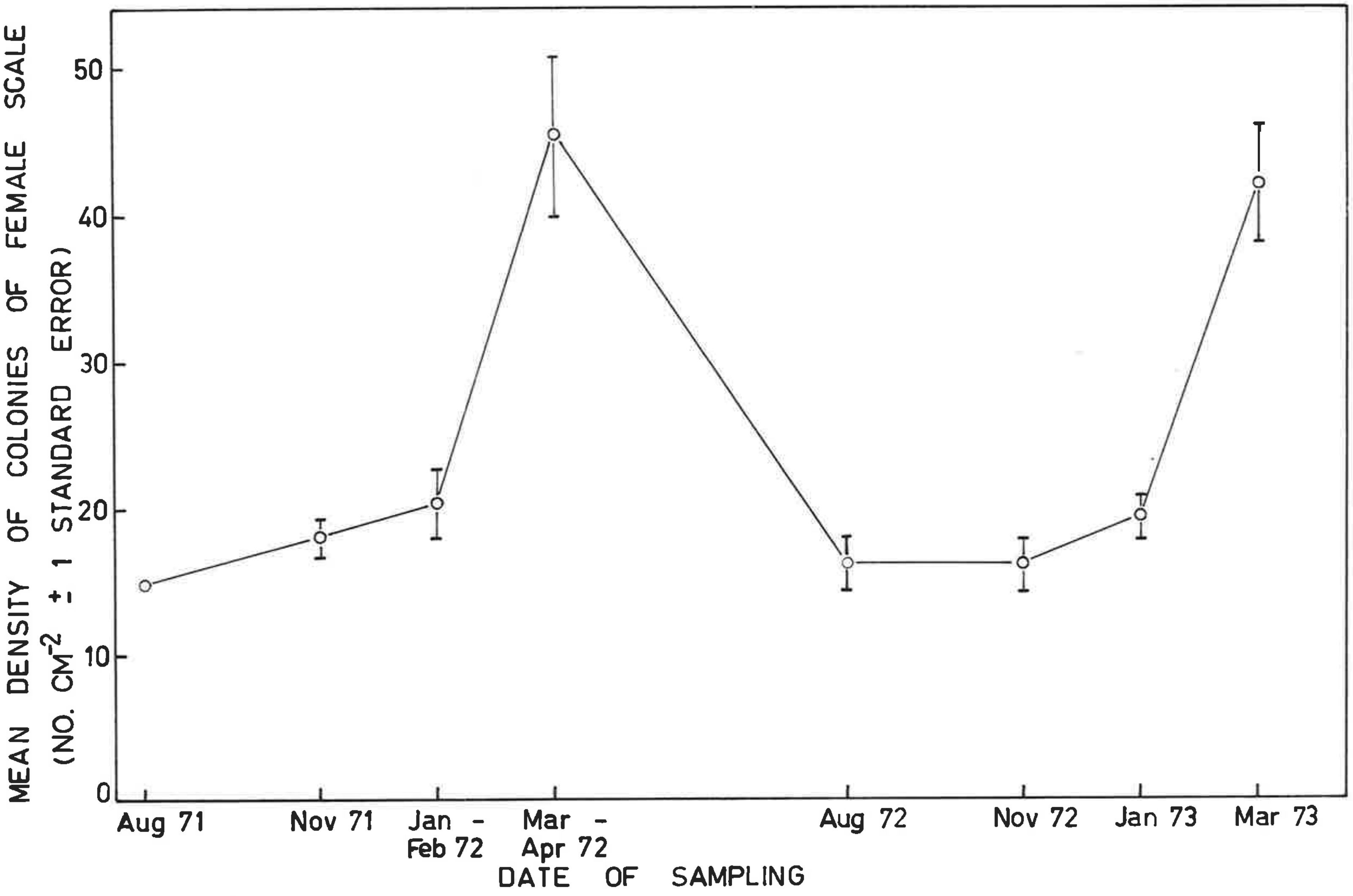
When large numbers of female scale settled on the leaves it was apparent that the leaves were not colonized at random. As part of a sampling programme five branches were chosen from the heavily infested tree previously mentioned (Obs. 1) in July 1972. The length of each leaf on those branches was measured and the number of scale on it noted. Overall 346 leaves were surveyed. As the leaf size increased so did the proportion of leaves with scale. There was also an increase in the mean number of scale per infested leaf as the leaf size increased (Table 2.1). The larger and older leaves are favoured. The majority (72.6%) of the scale settled on the upper-side of the leaves near the midrib or main veins. The basal section of the leaf is colonized first and the colony is extended towards the tip as newcomers arrive and settle.

2.2D Seasonal variation in the densities of the colonies of females

The newly moulted females usually space themselves quite regularly

Figure 2.5

Seasonal variation in the density of the colonies formed by female *E. coriaceus*.


MEAN DENSITY OF COLONIES OF FEMALE SCALE
(NO. CM^{-2} ± 1 STANDARD ERROR)
0
10
20
30
40
50
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
DATE OF SAMPLING

in the colonies they form so that even though each individual may increase in size several times (under favourable conditions) between settling and reproduction, it is assured of room in which to expand so that its ovaries can fully develop.

The necessity (and method) for measuring the densities of colonies will be discussed (3.1E). In some small populations the density was not determined as the scale were simply counted. There is a seasonal trend in the densities of the colonies, those in late summer being at least twice as closely packed (40-45 females cm^{-2}) as those at other times when the density is usually less than 20 females cm^{-2} (Figure 2.5; Table 4 Appendix).

The aggregations of E. coriaceus are very characteristic and it seems profitable to speculate on possible reasons for their formation.

2.2E Possible reasons for the formation of colonies

The aggregating behaviour of aphids has been the subject of many elegant and penetrating studies.

Colonies may confer nutritional advantages on the constituent individuals. In various species of aphids the rate of increase is maximal in small colonies of about 8-20 individuals (Way and Banks, 1967; Murdie, 1969; Dixon and Wratten, 1971). Way and Cammell (1970) examined the underlying mechanism and found that colonies of Brevicoryne brassicae on mature leaves of Brussells sprouts conditioned the leaves they fed on and formed powerful physiological sinks which diverted nutrients away from the growing parts of the plant (which are natural sinks). Thus an isolated aphid on the opposite side of the leaf from a small colony grew to a larger size (and was more fecund) than a single aphid on a leaf. Dixon and Wratten (1971) confirmed these findings on Aphis fabae. In small colonies the nutritional benefits are great and the aphids grow to a large size. As the number of individuals in the colony increases intraspecific competition dominates and the fecundity of the aphids rapidly decreases.

Many coccids also form aggregations but the benefits of such behaviour have not been examined in this group. Nevertheless it seems profitable to speculate on possible reasons for the formation of aggregations in E. coriaceus. One of the most likely reasons for the formation of colonies may be that insects in aggregations receive physiological benefits which those that settle singly do not receive.

It may be that the formation of colonies confers some advantage on the scale , for there does seem to be a connection between the physiology of the tree and the density of the colonies. The females are packed tightest together in late summer, often so tightly that their tests intermingle. Summers in Adelaide are hot and dry and therefore the time when the trees are most likely to be stressed.

When plants are subject to water stress at least two properties of some importance to homoptera may change. Firstly the turgor pressure of the plant is reduced and/or there may be an increase in the viscosity of the sap. The second factor is an increase in the soluble nitrogen in the sap (Kennedy, 1958; Kennedy and Booth, 1959). Other less important properties may also change and the interaction between the stressed plant and the homoptera may be complex (Kennedy, Lamb and Booth, 1958; Wearing, 1967; 1972; Wearing and Van Emden, 1967). If the homoptera relies heavily on turgor pressure to assist its feeding then it will not be able to benefit from the increased nitrogen. *E. coriaceus* has a great deal of control over food uptake (as shown by the increase in excretion, and thus uptake, when ants are in attendance). The increase in soluble nitrogen in the sap may enable them to settle more closely together in late summer because the area required for an adequate food supply will be less than at other times.

There was thus some hint of a physiological explanation of colony formation, and as *E. coriaceus* settle on mature leaves and on the twigs, I thought that here too physiological sinks might be produced (or the leaf conditioned) by aggregations of scale, giving the constituent individuals some advantage over isolated scale. To test this hypothesis I took one hundred leaves, supporting from 1-20 mature female scale, from one side of a small *E. cladocalyx* immediately before the scale began reproduction. The length of each individual scale was measured. The scale in these small colonies were not densely packed together so that their length ought to reflect their nutritional status. There was no indication that scale which occurred singly on the leaves were smaller than those which occurred in small colonies. Thus with colonies of these sizes there was no evidence that scale in colonies had any advantage over single scale. It is possible that colonies may confer physiological advantages on the constituent individuals but more comprehensive observations than those above would be necessary to demonstrate this.

2.2F Natural mortality to the adult female under favourable conditions

When predators are absent and conditions are favourable few female scale die between the time they settle and begin to secrete their tests, and the time they reproduce. The mean survival rate on four caged trees (*E. obliqua*, about 1.5 m high) in the Kuitpo Forest Reserve was 98.0%. The data for the trees are given below; on only one tree (No. 5) was the survival rate below 95% and several chrysopid larvae were removed from this tree. These larvae are highly dispersive and they apparently forced their way under the cloth skirt around the bottom of the cage. The data for this tree have thus been excluded from the analysis.

Survival of *E. coriaceus* females from beginning of test secretion to reproduction in field cages in Kuitpo Forest Reserve. December 1973.

Tree No.	No. females beginning to secrete tests	No. females alive at time of reproduction	% survival
1	99	96	97.0
2	352	352	100.0
3	190	189	99.5
4	136	130	95.6
5*	218	170	78.0

* Chrysopid larvae removed from this tree. Data excluded from analysis.

There were no high temperatures during the period of growth of the scale (September - December 1973). The trees were vigorous and well watered and there was no crowding in the scale populations. On one tree several scale were found covered with fungal hyphae but whether the fungus was the cause of death or infected them later is unknown.

2.2G Number of generations a year

Observations over the period August 1971 to July 1973 indicated that *E. coriaceus* had four complete generations a year. Near Alverstoke Orchard the generations were discrete and the approximate dates on which large numbers of young were first observed on trees, together with the number of days between successive bursts of reproduction, are shown below (Table 2.2). Summer generations take 50-55 days, the spring generation 85-90 days and the winter generation about 150 days.

TABLE 2.2 Times of reproduction and generation times.
Alverstoke Orchard.

Year	Date of reproduction and generation time
1971	August 20th; 91 days; November 19th; 58 days
1972	January 15th; 52 days; March 8th; 170 days; August 25th; 84 days; November 17th; 54 days
1973	January 9th; 51 days; March 1st; 139 days; July 18th

Reproduction in populations near Alverstoke Orchard was highly synchronized, both between populations on different trees and within a population on one tree. This synchrony is partly artificial for the populations observed after August 1972 were started by me in September 1972. Despite this, there was very close synchrony both within and between the populations from August 1971 to August 1972; also the population examined in 2.3B, where reproduction was synchronous, had been in existence for a year and one might have expected after this length of time that generations would be overlapping.

In the Mallee Block the situation was not so clear; I had some difficulty in determining the date of reproduction in some populations because of the small number of young produced, especially in summer. In the three populations examined between January and April 1972 generations tended to overlap but in August 1972 two of these populations (1842A and 1954B) consisted mainly of females which were beginning to reproduce. Generations were still overlapping in 1908B and many females had reproduced before August. Female scale in the two populations above (1842A and 1954B) reproduced in November. Predation reduced the populations so that by January very few females were present and hardly any young were produced between January and March.

Thus two of the three populations in the Mallee Block reproduced at approximately the same time as those near Alverstoke. On these trees generations were more or less discrete. One population had overlapping generations and was out of phase. In late July and early August 1973 six out of ten populations examined in the Mallee Block were composed either solely, or largely of females which were beginning to produce young but four populations contained all age groups.

My sampling plan was not devised to study the demography of the scale which I assumed, from my initial observations, was very simple in that generations were discrete and reproduction more or less synchronous. Patel came to a similar conclusion (Maelzer pers. comm.). While this was often true there were many populations which did not conform to this simple picture, reproducing at different times and with overlapping generations.

In summary, most of the scale present in winter are females and these reproduce in late winter or early spring; the next generation reproduces in late spring (usually November). Populations are greatly reduced after November (see Chapter 3) and generations tend to overlap in summer, reproducing twice before cool weather sets in (late April or May). The young females settle, develop slowly over autumn and winter and reproduce in late winter or early spring. _E. coriaceus_ is probably similar to the long tailed mealy bug (_Pseudococcus adonidum_) where few young are produced over winter and rising temperatures in spring cause a broad synchronization of generations (Furness, 1973).

In any future study of _E. coriaceus_ the demography of a large number of populations ought to be examined. To do this frequent destructive samplings ought to be performed and this may be difficult without destroying many small populations entirely.

These observations differ from those of Patel (1971) who worked in the same area and claimed that the scale had five complete generations a year. He stated that the winter generation lasted for 85 days. This was not so during the period I observed the scale as the winter generation took about 140-170 days (probably depending on when reproduction began in autumn). The scale completed development in 85 days in spring but this was with swiftly rising temperatures in October and November. The greatest number of complete generations I observed was four. In 1973 a partial fifth generation occurred in at least one population for the females reproduced in mid-July whereas in the previous year they had reproduced in August (see table above). Perhaps the populations which reproduced in mid-winter 1973, and were out of phase with the ones I observed, had five or nearly five generations a year.

2.3 Comments on fecundity and reproduction

2.3A Fecundity and the influence of the length of the female on the number of young produced

The size of the female insect is often an accurate indication of the number of young she can produce (Southwood, 1966, page 241). Either weight or body length may be used. Patel (1971) demonstrated that length is a good indication of the fecundity of female *E. coriaceus* (see comment on length in 1.6C). The following observations confirm his work and demonstrate that the number of embryos contained by the female immediately before reproduction also gives a good estimate of fecundity. This latter relationship is used in observations on the effect of crowding on fecundity (6.1D).

Materials and Methods

Infested leaves were collected from three adjacent trees (*E.*

cladocalyx) in November 1971. The females were about to reproduce and most began laying after a few days in the laboratory. Because each tree produced only a few suitable leaves with female scale, all the leaves were pooled.

Female scale from the leaves were used as it was an easy matter to make leaf discs (see below) and individual females could be kept alive until they had completed reproduction. Although many young may be produced from females isolated on cut sections of twigs (2.4) there is not the same certainty that the females will survive long enough to complete reproduction as there is with scale on leaf discs.

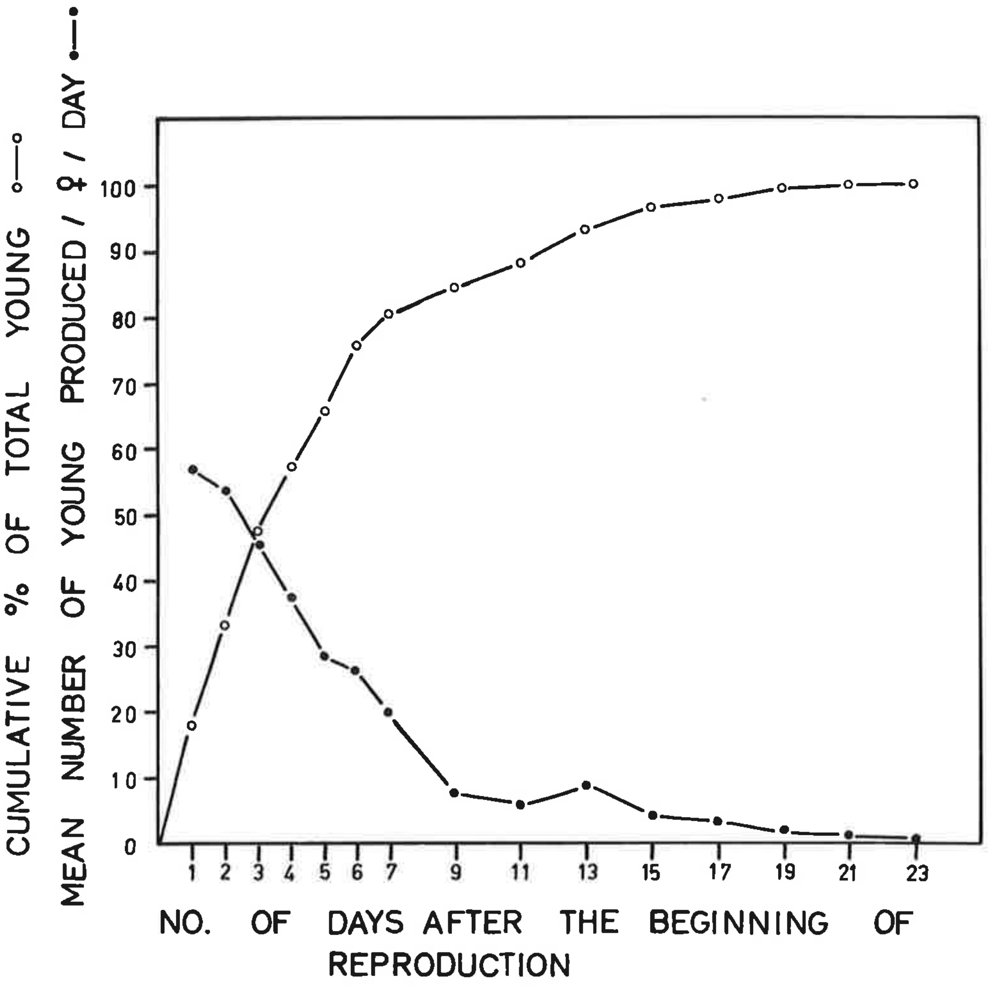
The female scale were randomly divided into two groups. One group was used to assess fecundity. Females of the other group were measured, removed from the leaf to alcoholic Bouin's Fluid (Duboscq-Brasil Fixative, Pantin, 1964) for several hours for fixing and then transferred to 90% alcohol. They were later dissected and the number of embryos they contained determined.

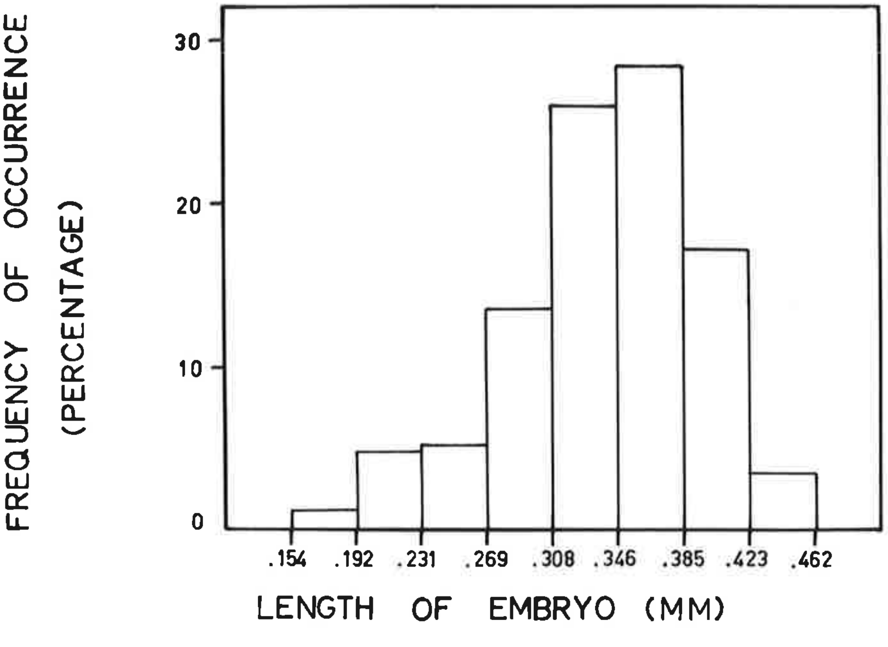
In the first group an area of leaf surrounding one or more female scale was punched out, using a cork borer 2 cm in diameter, so that a leaf disc bearing the scale was obtained and could be floated on water in a plastic vial. The outer lip of the vial was coated with vaseline in case any crawlers should leave the disc if it touched the side of the vial. The discs were placed at 25°C (± 2°C) under strong fluorescent lights to maintain photosynthesis in the leaf disc (12 hour photoperiod). If more than one female occurred on a leaf one was chosen which would extend the range of size of those under observation; if all the scale on a leaf were of about the mean size one was chosen at random. The

Figure 2.6

(a) The mean number of crawlers produced per female per day during reproduction at 25°C and the cumulative percentage of young produced under these conditions.

(b) The frequency distribution of the lengths of embryos dissected from five females about to reproduce (July, 1973).


CUMULATIVE % OF TOTAL YOUNG ○—○
MEAN NUMBER OF YOUNG PRODUCED / ♀ / DAY ●—●
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
9
11
13
15
17
19
21
23
NO. OF DAYS AFTER THE BEGINNING OF REPRODUCTION


FREQUENCY OF OCCURRENCE (PERCENTAGE)
0
10
20
30
.154
.192
.231
.269
.308
.346
.385
.423
.462
LENGTH OF EMBRYO (MM)

others were measured and removed to fixative.

As each female began to reproduce, her length was measured. The removal of the discs from the water surface was hazardous and many sank when they were being replaced. The young were counted, in situ, on the disc each day, so obtaining a cumulative total for several days until the disc was crowded and the young could not easily be counted. The disc was then removed and all the young taken off with a camel hair brush and counted. The disc was replaced on the water and the process repeated after several days.

Daily counts were made on 25 discs initially (7 of which sank) and continued for 7 days after oviposition began; after that counts of the young were made every other day. On another 11 discs the young were removed and counted only once at the conclusion of the observations.

The results from both groups are pooled and used to calculate the regression equation for the influence of size on fecundity.

Results

The length of the females and the number of young they produced are given in Table 5(a) (Appendix). The regression of fecundity on size is highly significant ($F_{1,\ 26} = 38.282$, $p < .005$); the equation was calculated as $y = 309.16x - 494.74$ where y = number of offspring produced per female; x = length of the female scale in mm.

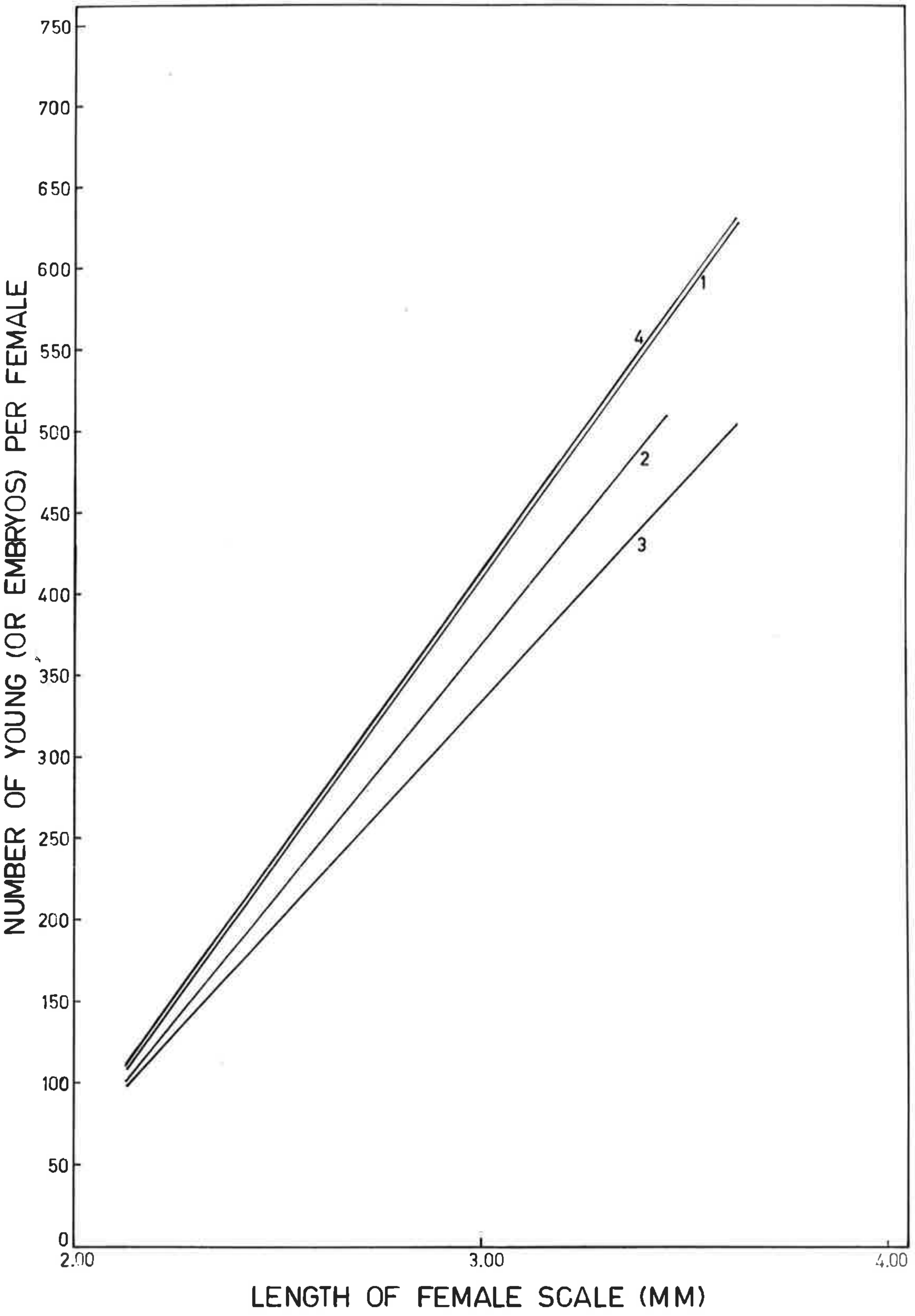
Once females begin to lay, reproduction proceeds quickly. At 25°C, 81.2% of total offspring were produced after 7 days. Figure 2.6(a) shows the mean rate (cumulative percentage) of reproduction and the mean number of young produced per female per day.

After 23 days oviposition ceased and the scale were dissected.

Figure 2.7

The relationship between the size of the reproducing female and her fecundity, and also the number of embryos she contains.

1. The relationship between size and fecundity, present study. $y = 309.16x - 494.74$
2. The relationship between size and number of embryos. $y = 305.87x - 550.10$
3. The relationship between size and fecundity derived by Patel (1971). $y = 277.31x - 502.41$
4. Patel's line corrected on the assumption that he measured only 80% of the young produced (see text).


750
700
650
600
550
500
450
400
350
300
250
200
150
100
50
0
NUMBER OF YOUNG (OR EMBRYOS) PER FEMALE
1
4
2
3
2.00
3.00
4.00
LENGTH OF FEMALE SCALE (MM)

Most (20) of the 28 scale were dead. The survivors were drying out and had very few embryos. Embryos contained at this time were only 2.6% (SD 5.8%) of the total number of young produced.

Patel's (1971) data are not expressed in a form which allows a ready statistical comparison with mine. The two lines are of obviously similar slope (see Figure 2.7) although the elevations are probably different. In his paper he states that oviposition continues for a week. If it is assumed that he stopped his observations at this time (i.e. after only 80% of the total offspring were produced) the true fecundity can be calculated. The agreement between the total number of young produced per female on Patel's corrected data and mine is then very close indeed (Figure 2.7).

The size of the female scale and the number of embryos she contains immediately before reproduction (Table 5(b) Appendix) are also related, the regression being highly significant ($F_{1,\ 28} = 93.10$, $p < .005$). The relationship may be expressed by the equation $y = 305.87x - 550.10$, where y = number of embryos the female scale contains; x = length of the female scale in mm.

A comparison of the two regression lines for the influence of female size on fecundity and on number of embryos contained shows that the slopes are identical but that the elevations are quite dissimilar (comparison of slopes: $F_{1,\ 54} = .003$ N.S.; comparison of elevations, $F_{1,\ 55} = 10.751$, $p < .005$). Thus the number of embryos present immediately before reproduction represents 85% of the number of young that may be eventually produced. An examination of the frequency distribution of sizes of embryos at this time (Figure 2.6(b)) shows that the distribution is skewed and many embryos are well developed and must quickly pass through the final maturation period. Embryos over 0.385 mm are almost ready to be laid. (Date for 250 embryos, 50 chosen at random from five female scale, July 1973).

Reproduction in *E. coriaceus* is thus typical of that of the soft scales and pseudococcids which produce many eggs or young over a short period. Bodenheimer (1951) examined many soft scale and found that *Ceroplastes floridensis*, *Pseudococcus citri* and *Saissetia oleae* all had reproductive periods of less than 30 days even in cool weather, and during this time usually laid at least 200-300 eggs. These scale often contain a large proportion of the total number of eggs before they reproduce (Bodenheimer, 1951).

On the other hand Willard (1972) reared red scale, *Aonidiella aurantii*, a typical armoured scale, in the laboratory at different temperatures. He found that females at 30°C produced most young and at this temperature the mean period of reproduction was 106 days. The mean number of young produced per day was 2.55 (range 1.34 - 4.17) and at lower temperatures reproduction was extended. Bodenheimer (1951) gives similar low rates of production of crawlers per day for *A. aurantii* and other diaspidids.

2.3B *Reproduction in the field, July-August 1973*

The rapid production of young was not restricted to scale under laboratory conditions for reproduction was often synchronized within the population on a tree. The branches were soon covered by the minute crawlers which appeared as a fine red dust as they wandered in search of a place to settle. Kirk (1908) mentions this as a notable feature of this scale in New Zealand. Although the rapid production of young had been demonstrated by an examination of the ovaries of the female scale (1.6C) and I had observed it on many occasions, I wanted to measure accurately the rate of recruitment of crawlers. I was also curious to see whether reproduction might not be synchronized by spells of warm weather occurring at the end of winter.

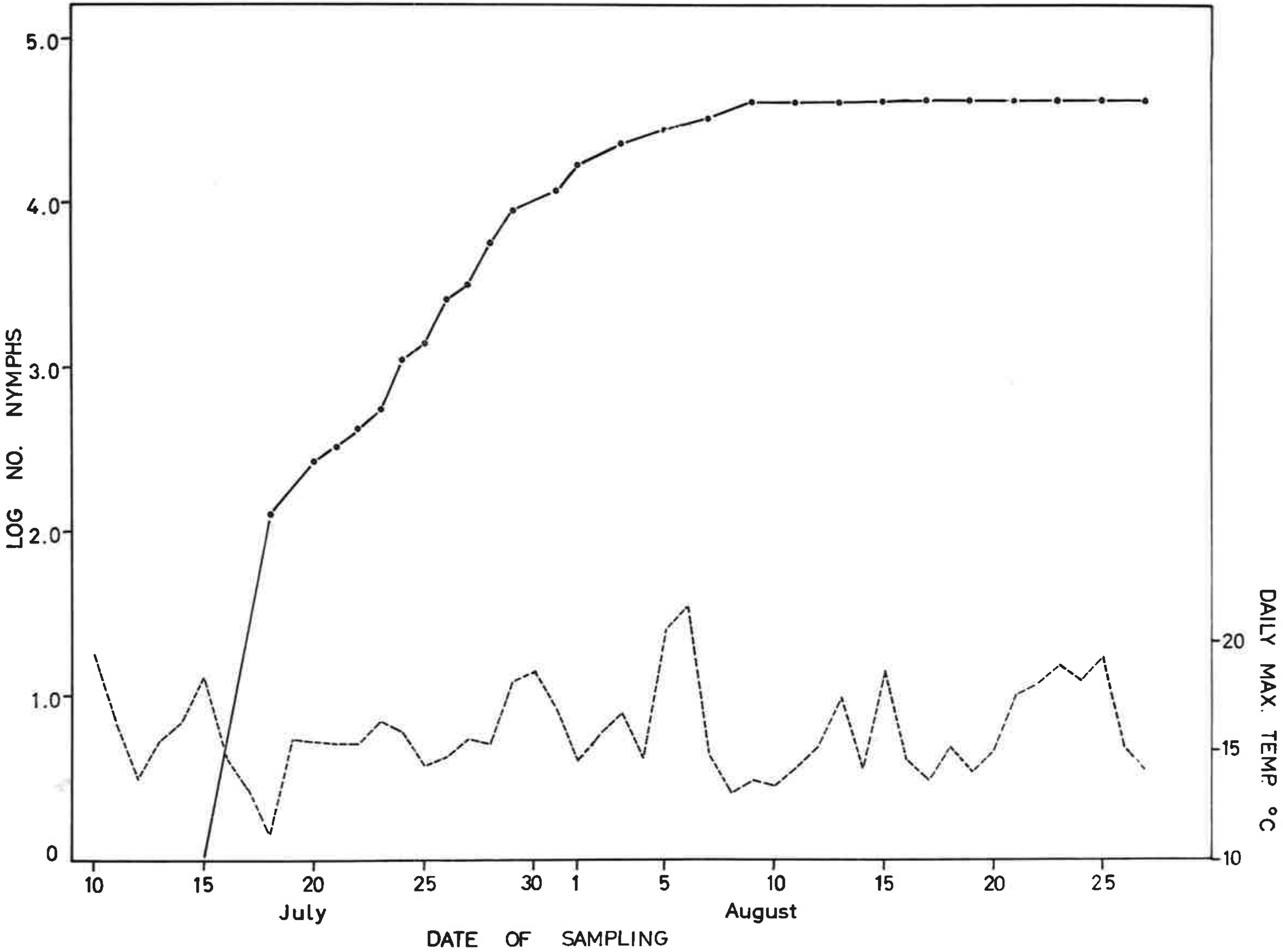
In June 1973 a population of females was chosen which had developed from crawlers produced in March 1973. When observations began in June the population consisted entirely of adult female scale; these females began reproducing in July and continued through August. The log cumulative number of crawlers that settled on the tree is shown in Figure 2.8 and it can be seen that young were produced quickly and synchronously.

The number of first instar crawlers was estimated by measuring the area they covered, by estimating their mean density and multiplying the two. The mean density of the nymphs was measured by removing bark slivers covered with first instar nymphs; small areas of these colonies were then delineated using a squared graticule in a binocular microscope and the number per unit area determined. The mean density was estimated as 669 nymphs cm^{-2} (S.D. 11.2; 5 samples). From 18th July until 1st August a daily tally of the young was kept; after 1st August counts were made every other day.

During this period the only deaths among the young were caused by rainfall and wind. To measure loss to rainfall two traps (rectangular trays 25 x 20 cm with a fine gauze bottom) were placed beneath large colonies to catch dislodged immature scale. The sides of the traps were coated with grease to prevent crawlers escaping. The traps were placed directly below the colonies of immature scale. The scale in the traps were removed every one or two days and the number of scale in the colony above the trap estimated. From 31st September until 7th August (when the traps were removed) they collected a small percentage of the nymphs, 1.2% and .9% of those in the colonies above the traps. During this time 13.0 mm of rain fell. On 8th August there was a violent windstorm with gusts up to 56 km/hour but with only 2.8 mm of rain. An examination of the colonies next day (when the area covered by scale was measured) showed that 52% of the area covered by crawlers had been destroyed. Many leaf edges were stained with the "blood" of the scale, indicating that immature scale were not washed off the tree but were killed by leaves being whipped against the colonies by the high winds. Traps were immediately replaced from 8th August to 16th August, and 4.3% and 9.6% of the nymphs in the colonies above the traps were collected (20.9 mm of rain fell during this period). Two traps set under colonies on another tree during this period collected 1.3% and 2.6% of the nymphs in the colonies above. As far as I could determine rainfall had little influence on the crawlers, producing an overall loss of less than 10%. Wind drastically reduced the population on one tree but two other populations examined in the Mallee Block after the

Figure 2.8

The settling of crawlers produced by a population of female *E. coriaceus*, July and August 1973. The daily maximum temperatures during reproduction are shown.


5.0
4.0
3.0
2.0
1.0
0
LOG NO. NYMPHS
DAILY MAX. TEMP. °C
20
15
10
10
15
20
25
30
1
5
10
15
20
25
July
August
DATE OF SAMPLING

storm did not show any evidence of the effect of wind; therefore the effects are likely to be local. Wind and rainfall have negligible effects on the adult scale which is protected by her test.

The data used in Figure 2.8 have been corrected for these sources of mortality, and represent, as accurately as possible, the number of young produced. The total number of young was estimated as 42,300.

The number of young settling on the tree increased from 15th July until 9th August after which there was only a relatively small number of young added to the population. (Note. As the rate of recruitment was measured by the increasing areas covered by the first instars it is obvious that the number of young produced on the 8th and 9th of August could not be measured as many young would have been washed away before they before they settled. I have thus assumed that young were added to the population at the same rate as in the immediately previous period of the same duration). Although the decrease in the rate of recruitment of young coincided with the massive mortality caused to the young by the storm, there was no evidence that the storm harmed any of the female scale and I believe these occurrences not to be connected. The reproductive period was therefore relatively short (approximately 30-35 days) even in this cool weather where the daily maxima were often about 15°C and the highest value was 21.1°C. There was some evidence of a few young being produced even after 27th August but they were in very small numbers. Reproduction seems therefore relatively little influenced by temperature, large numbers of young appearing on the trees during and after cold weather (e.g. some of the coldest weather occurred from 15th - 18th July yet young were produced then).

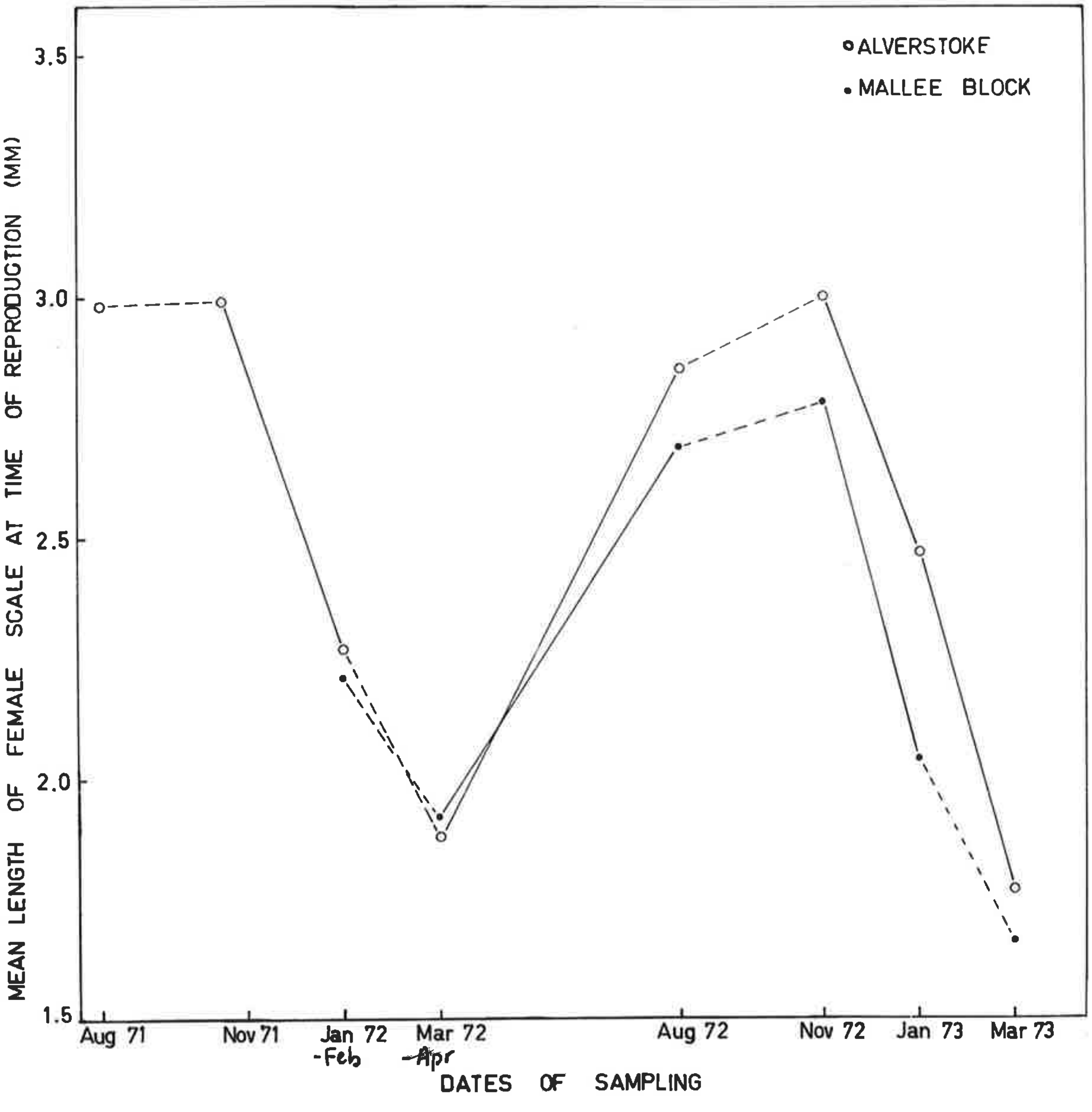
The number of female scale on the tree was counted and a large sample removed in late August to determine the mean size of the females and to estimate the number of scale that had reproduced (there was very little increase in mortality to the females from 18th July to 29th August as there were no predators and few parasites in the area). Of the total population of 152 females, 105 were removed and of these 77 had reproduced; it was estimated that 110 females on the tree had reproduced. The mean size of the females was 3.34 ± .12 mm (mean and Standard Deviation). The number of young produced per female was estimated as 384.5 (calculated by dividing the total population of crawlers by the number of females that reproduced), whereas the number anticipated in accordance with the relationship $y = 309.16x - 494.74$ was 539.7. The discrepancy is large, 155.2 young or 28.8% of the total young expected. The reason for the discrepancy is not known. The size of the females was extremely large compared to those on which the regression of size on fecundity was determined, and the parameters of the regression equation may change for different populations. Bodenheimer (1951) found that a large proportion of young of *A. aurantii* were blown away by the wind. It is known that *E. coriaceus* is distributed by the wind (Kirk, 1908; Clark, 1938) and it may be that many were blown away from the tree as the weather was very windy.

2.3C Seasonal variation in the length of the female scale at the time of reproduction

As part of the method of sampling for mortality (described in 1.6B)

Figure 2.9

Seasonal trends in the mean length of the reproducing female scale for two areas at the Waite Institute. (Those values which differ significantly are joined by entire lines.)


○ ALVERSTOKE
● MALLEE BLOCK
MEAN LENGTH OF FEMALE SCALE AT TIME OF REPRODUCTION (MM)
3.5
3.0
2.5
2.0
1.5
Aug 71
Nov 71
Jan 72
-Feb
Mar 72
-Apr
Aug 72
Nov 72
Jan 73
Mar 73
DATES OF SAMPLING

lengths of surviving females in the sample on each bark sliver were measured. The length of the female at the time of reproduction is related to the number of young she is able to produce.

There was significant variation between some samples collected at the same time from the population on a tree. This non-random size distribution within a population is probably caused by localized crowding. Finney's recommendation (Laughlin, 1967) was therefore followed and the unweighted means for the samples were used.

Tables 6(a) and (b) (appendix) show the mean size of scale for the populations near Alverstoke Orchard and in the Mallee Block with significant differences marked. These findings are summarized in Figure 2.9.

In both areas there is a marked annual cycle in the length of the females with large individuals produced in winter and spring, smaller ones in early summer and very small females in late summer and early autumn. The scale on all the trees show a decline in size from January to March 1972, and although the trend is not significant within each set of trees, over the six trees there is a significant decrease in the lengths of the females, ($t = 3.467$; 4d.f.; $p < .05$). There was no significant difference in the lengths of the female scale between August and November 1972.

Bodenheimer (1951) observed the seasonal variation in fecundity of soft scales in Palestine which has a climate similar to that of Adelaide, with hot dry summers and winter rainfall. He found that in *Ceroplastes floridensis* there were autumn and spring peaks in the number of eggs per female; *Mytilococcus beckii* also had a lower fecundity in summer. Although *Pseudococcus citri* produced most eggs in warm weather its fecundity was highest at 21°C, decreasing when the scale was reared at 17 or 25°C. *Icerya purchasi* had a seasonal cycle in fecundity almost identical to that of *E. coriaceus* with maximum fecundity in early spring, decreasing to the lowest values in autumn. *I. purchasi* is a native of Australia and is commonly found in Adelaide where it almost certainly has an annual cycle in fecundity similar to that in Palestine and for *E. coriaceus* in Adelaide.

The fecundity of the armoured scales is more difficult to assess for unlike the soft scale the number of eggs a female contains is not necessarily closely related to her overall fecundity. Willard (1972) found female red scale (*Aonidiella aurantii*) which developed at a constant temperature of 30°C more fecund than those reared at 25 and 20°C and found that those at the highest temperature produced about six times as many young as females reared at 15°C. This is a rather surprising result as 30°C is a high mean temperature.

Murdie, in his laboratory studies on *Acrythosiphon pisum* found that at temperatures above 15°C the size of the aphid decreased (Murdie, 1969a) as did its fecundity (1969b). He cites many references showing that increased rearing temperatures caused a decrease in the size of organisms (1969a) and also, in his latter paper, Messenger's (1964) experiments demonstrating that *Therioaphis maculata* was most fecund at a mean temperature of 16°C (fluctuating conditions with a diurnal range of 11°C).

It would seem therefore that *E. coriaceus* is in no way unusual among the homoptera in having a seasonal cycle of fecundity with the smallest females being produced in early Autumn because they have developed under very hot conditions in late summer. The consequences to the population are discussed later (3.4). The difference between the soft scales and the diaspidids becomes apparent once again, perhaps indicating the specialized nature of the latter group.

2.4 Seasonal variation in the sex ratio of the young.

Although the sex ratio in organisms utilizing X and Y chromosomes and random assortment should in theory be 1:1, variations in the primary sex ratio of the young may occur (Yanders, 1965). However in such organisms these variations seem neither common nor pronounced.

In organisms where sex is determined in a less orthodox manner, variations in the sex ratios of the young are more common. This is particularly so with the coccids which have atypical genetic systems.

Early in the study it seemed likely that the sex ratio of the young, percentage of the total young that were females, (in the field) varied between seasons. Two times were chosen to examine the sex ratio of the young when it was expected to vary most. These were spring (August and September) when the females were very large and had developed under cool conditions with vigorous plant growth, and late summer (February and March) when the females were small and developed under extremely hot dry conditions. At the appropriate time trees were chosen which had uncrowded populations of female scale (as population density may have some influence on the sex ratio of the young produced). When the

TABLE 2.3 Seasonal variation in the sex ratio of the young of *E. coriaceus*.

September 1973

Total number of young examined	% ♀
900	71.1
1,753	77.2
3,632	70.1
453	78.6
1,006	71.6
Mean % females	73.72

March 1973

Total number of young examined	% ♀
288	66.7
1,058	55.0
2,924	50.4
4,646	61.8
1,605	56.7
Mean % females	58.12

first crawlers appeared sections of twigs containing a small number of females were cut from the tree. The leaves were removed, the cut ends of the twig waxed to prevent water loss and the twig sections tied to a potted tree. On these excised twig sections female scale will survive for many days and readily produce crawlers. These settle on the potted trees and their sex can be determined when the male pupae have been formed.

Samples were removed from five trees at each sampling date. Table 2.3 shows the complete data for the two sampling times. The sex ratios decreased from 73.7% in spring to 58.1% in summer ($t = 4.713$, 8 d.f.; $p < .005$). The sex ratio of the young produced in November appears to be similar to that in August - September. The sex ratios of young (and total number of young examined) from uncrowded trees in November 1971 and November 1972 were respectively 63.6% (1542); 72.8% (1991); 70.2% (1830).

As there were no suitable controlled conditions in which to raise the young they were reared under prevailing weather in cages. It is possible that the change in sex ratio may be due to differential larval mortality but this is not likely for although the temperatures are higher in April than in October they are not excessive (temperature range in cage up to 20^{o}C).

2.4A A discussion of the methods of sex determination in coccids

There are two evolutionary series in the coccids, one containing the most primitive coccids, the Margaoidae and the other series the

Lecanoidae and Diaspidoidae (Balachowsky 1942, Jancke 1955, Theron 1958. I have not seen the paper by Balchowsky). The genetic system of the primitive coccids (XX-XO) is the same as that in the Sternorhynca (Hughes-Schrader 1948). The male coccids in the other evolutionary branch have three unusual genetic systems (the diaspidid, the lecanoid and the Comstockiella). Throughout the coccids the females are normal (Hughes-Schrader, 1948).

In the diaspidid system if the paternal chromosomes are eliminated during early embryogenesis the embryo develops as a male which is haploid. Spermatogenesis consists of a single mitotic division both products of which yield sperm (Brown and Bennett 1957, Bennett and Brown 1958).

In the other two systems the early embryonic stages are indistinguishable. One set of chromosomes, the paternal (Nelson-Rees, 1960), becomes heterochromatic at the blastula stage in the male embryo and remains so during development. The difference between the two systems becomes evident at spermatogenesis (which takes place towards the end of the second instar) (Hughes-Schrader 1948; Brown and Nur 1964; Brown 1963, 1965). Brown and McKenzie (1962) summarize these different systems.

Brown (1967) examined a number of genera of Eriococcidae and found a wide variation in genetic systems from lecanoid to typical Comstockiella. These results showed the wide affinities of the family which had previously been indicated from a taxonomic point of view (Hoy 1963). Among the species examined was _E. coriaceus_ which was found to have a typical Comstockiella system (ibid.).

Although the male breeds as a haploid individual, males and females alike develop from fertilized eggs. Thus sexual differentiation among the embryos must be under the control of the ovarioles of the female. The physiological condition of the female at the time of fertilization has a profound influence on the sex ratio of the young produced. If fertilization is delayed the sex ratio of the offspring changes (James 1937, Nelson-Rees 1960). Conditions of high humidity (James 1938) or high temperature (Nelson-Rees 1960) cause an increase in the proportion of males born. Between species and within species the variation in the sex ratio of young produced from pseudococcids is very great (James, 1937; 1939) providing further evidence that sex determination is unstable and modifiable by environmental influences.

Despite the variability of the sex ratios of cohorts of young from laboratory studies there seem to be few records of seasonal variations in the sex ratios of coccids in the field. One difficult in measuring the sex ratio of scale in field populations is that the males are often present for only a short time whereas the females are often long-lived. Care must also be taken to avoid confusing differential mortality with changes in the sex ratio of the young at birth. Bodenheimer (1951) reared cohorts of young and determined the ratio of the sexes. He found that in some species the proportion of males increased in summer. In *Pseudococcus citri* many males were produced (in Palestine) in June and September, the times of the hamsin winds. Bodenheimer's data for *A. aurantii* show a similar significant increase in the proportion of males in summer (June and July). On pages 216 and 217 Bodenheimer reports work by Quayle in California (no direct reference) and Jones (1936) in Southern Rhodesia. Both found an increase in the proportion of males in winter (I have not seen Jones' original paper). The problem with these last two studies is the small number of offspring examined and the high variability. Mahdihassan (1963; 1964) noted massive changes in the sex ratios of young lac insects (particularly *Lakshadia mysorensis*). He found that females which developed in the wet season produced almost entirely male young whereas those which developed in the dry season produced a strong preponderance of female young. Graham and Prebble (1953) found no variation in the sex ratio (64% female young) of *Eulecanium coryli* over several years but Glendinning (1925) recorded that females sometimes comprise only a quarter of the adult lecanium population. Hausermann (1966) found variations in the sex ratio of young from different generations of *Planococcus citri*. On the other hand, Habib *et al*. (1970) recorded a steady sex ratio over three successive generations in the field for the plum scale *Parlatoria oleae*. About 70% of the young were females.

It would thus appear that sex ratios in coccids are highly variable and it seems likely that further investigations would reveal more cases of seasonal variation in the sex ratio of the young.

2.5 Life history of the male

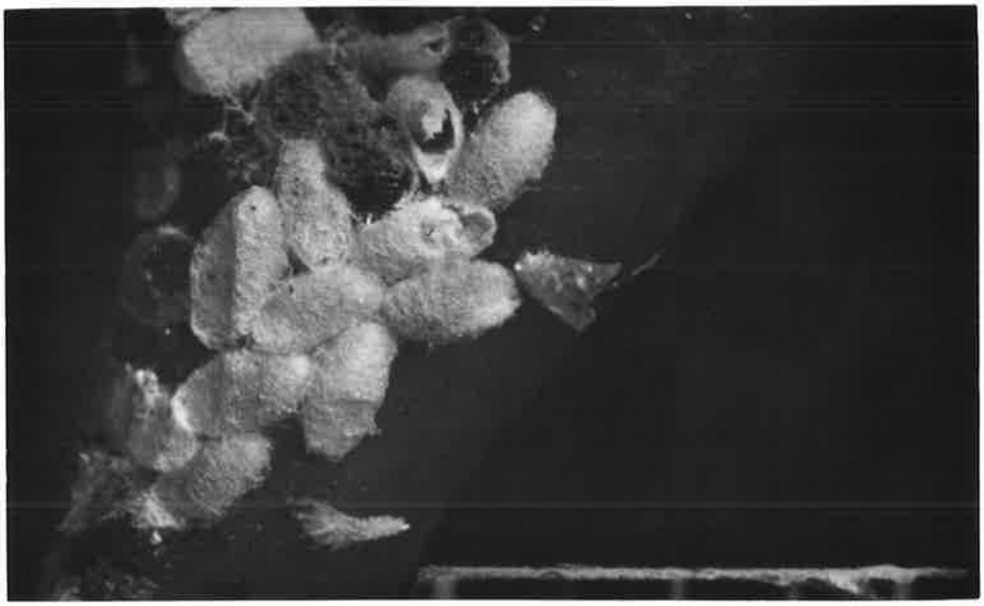
2.5A General Biology

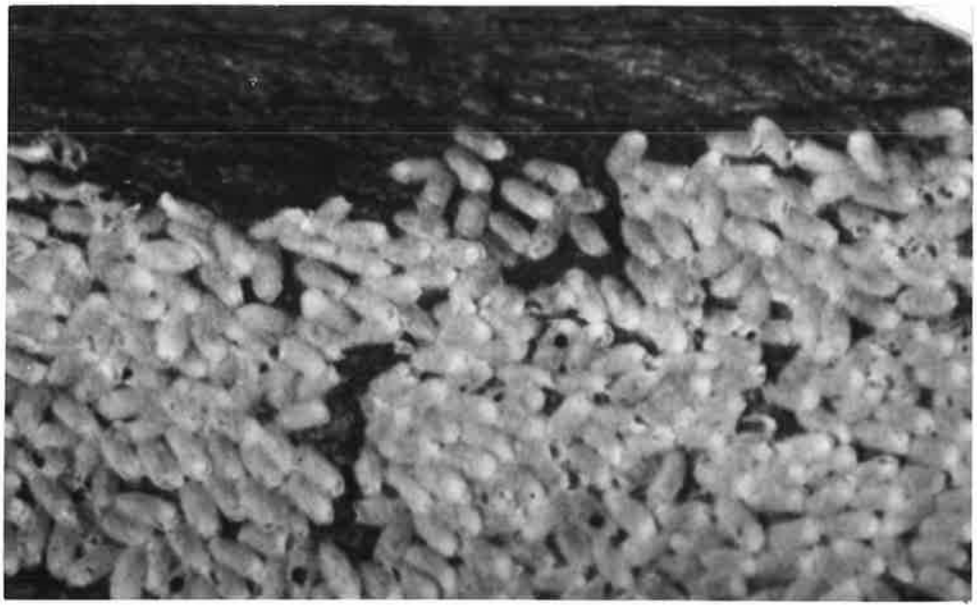
Both sexes start feeding after the first moult. The test of the

Figure 2.10

(a) Male pupal cases

(b) An aggregation of male pupal cases on the lower stem of a tree.





male is cottony, white, elongate and encloses the entire body (see Figure 2.10(a)). The male becomes more elongate than the female larva and after about eight days at 20°C a moult occurs and the exuviae are cast through the caudal slit. The pupal stage has no mouthparts and the wing buds become obvious as small vesicles on the mesothorax. The pupal stage lasts about four to five days at 20°C and the adult emerges two to three days later. During this last stage long waxy caudal filaments are protruded through the caudal slit. The males back out of the sac with wings fully expanded (if they are not brachypterous) causing the caudal slit to gape open, a characteristic feature of aggregations of pupae from which the males have emerged (Figure 2.10(b)). The males wander widely over the tree and fertilize the newly moulted females either in the newly forming colonies of females, or before the females move off from the feeding sites they occupied as second instars.

Patel (1971) describes the biology of the male and the following comments are from his paper. Virgin females respond to the male by lifting the terminal abdominal segments as the male examines her. Copulation lasts usually for five to ten minutes, and one male may mate with up to 12 females (the females mate once).

Male coccids commonly mate with more than one female; James (1937) found that males of Pseudococcus citri (Risso) could mate with up to 23 females. This is presumably necessary because many coccids under ideal conditions have a sex ratio balanced very much in favour of females.

The males live only two days.

Figure 2.11

Males of E. coriaceus.

The upper photograph shows a brachypterous male (left) and a male with wings of intermediate length (note that the wings do not reach the end of the abdomen).

The lower photograph shows a male with wings of intermediate length (left) and a macropterous male (note that the wings protrude beyond the end of the abdomen).

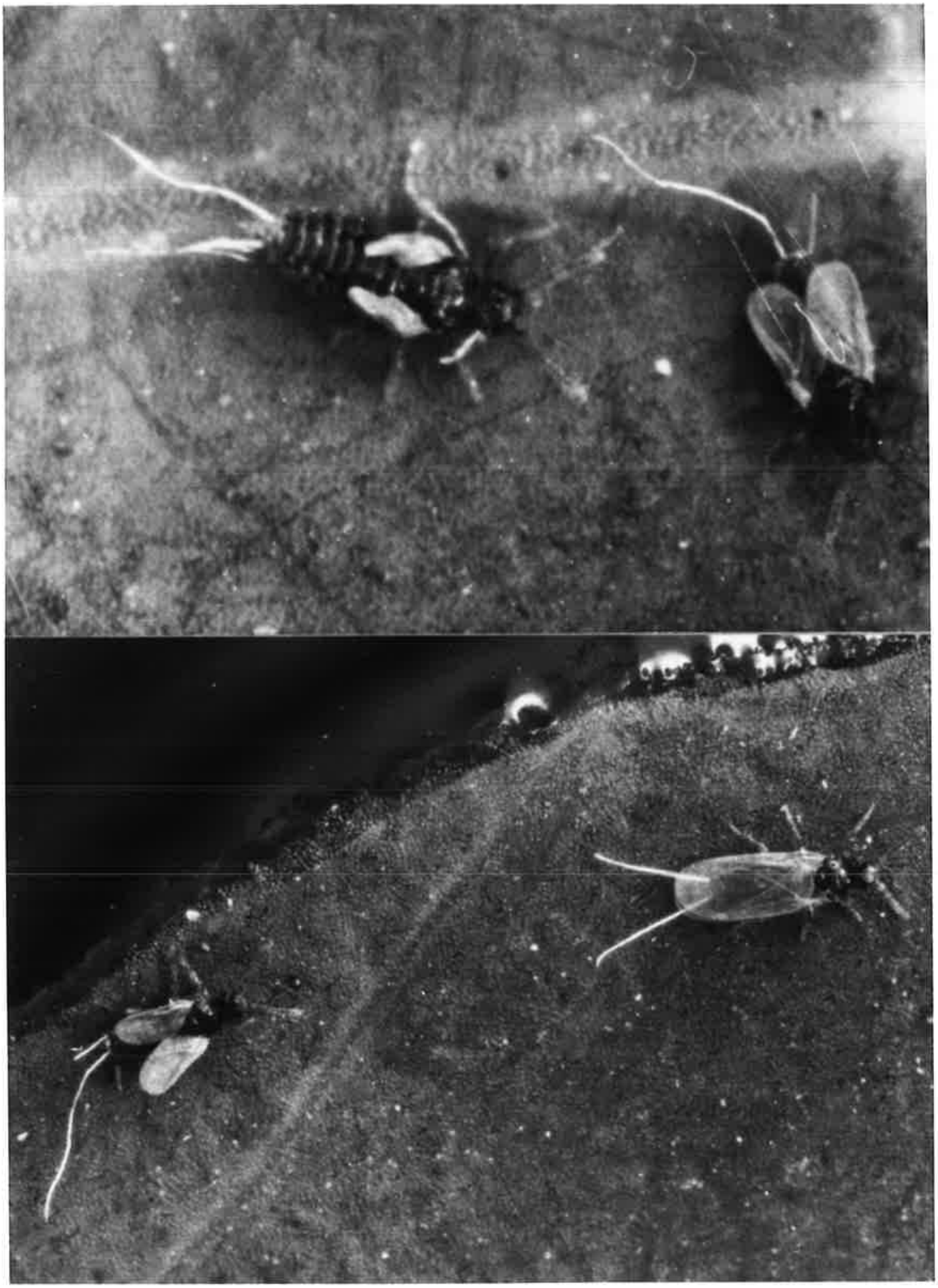


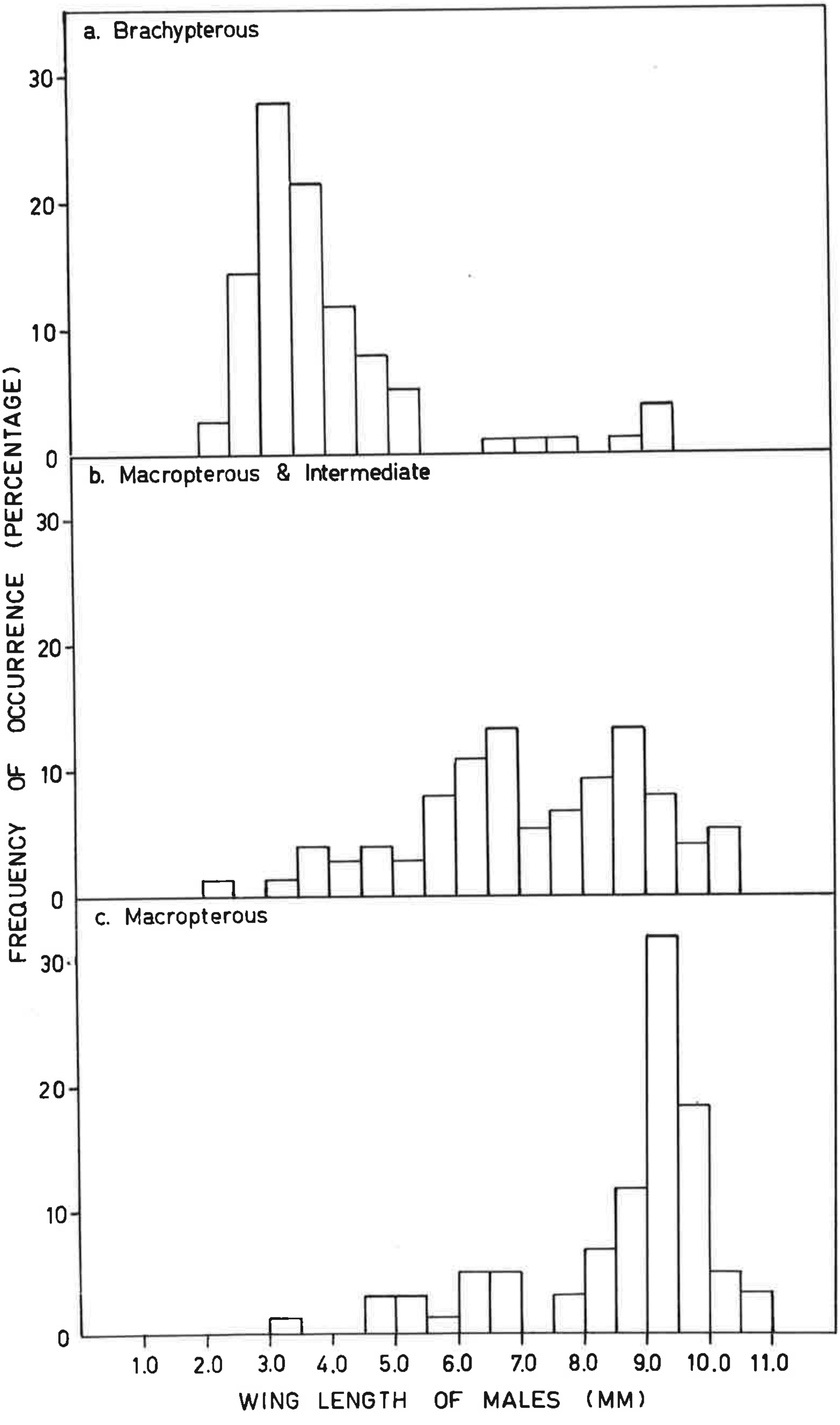
Figure 2.12

Frequency distribution of wing lengths of male *E. coriaceus*

(a) Predominantly brachypterous (76 males measured)

(b) Intermediate and macropterous (49 males measured)

(c) Predominantly macropterous (74 males measured)


a. Brachypterous
b. Macropterous & Intermediate
c. Macropterous
FREQUENCY OF OCCURRENCE (PERCENTAGE)
0
10
20
30
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
10.0
11.0
WING LENGTH OF MALES (MM)

2.5B Wing forms in the male

Patel's illustration is of a long-winged male and I was surprised to notice that brachypterous forms also occurred.

Collections of males were made from populations at the Waite Institute and at Kuitpo Forest Reserve. The males were taken whilst they were actively walking over the tree. They were removed from the tree with a fine brush and preserved in 70% alcohol. The wing length, body length (from head to the tip of the style) and width of the head capsule were all measured for each specimen to the nearest .01 mm. The number of antennal segments was also counted.

Initially a series of 10 males was measured on a wet slide under a stereo microscope. A fine brush was used to draw out the wings. If the wings did not lie flat two cover slips (one on top of the other) were placed beside the specimen and a wing spread on these. The other features were easily measured. These males were then cleared, stained and mounted individually under cover slips so that more accurate measurements of the wing length could be made under a compound microscope. There was no significant difference between the wing lengths for individuals measured wet or on slides (t test on the paired measurements). As the former method was simplest and did not distort body length it was used for the subsequent measurements.

The frequency distributions for wing lengths from three sets of populations are shown in Figures 2.12(a), 2.12(b) and 2.12(c). There are three commonly encountered forms if classified by wing length. The brachypterous form is demonstrated in Figure 2.12(a) lower mode; truly macropterous form in Figure 2.12(c) upper mode, and intermediate form in Figure 2.12(b) lower mode. In each population the distribution of lengths are bimodal or tend towards bimodality.

The three wing form are illustrated in Figure 2.11. Brachypters may have either fully expanded but short wings, or longer wings, probably of the intermediate type, but not fully expanded. True brachypters are the most common form in those populations composed chiefly of the short-winged males and even in the lower mode of the chiefly long-winged population (Figure 12.2c). Only two out of the nine had wings which were not fully expanded. The wings of the brachypters are usually below .5 mm in length and of coarser texture than in the other two forms where the wings are exceedingly fine. Macropterous forms have wings longer than .8 mm which usually reach or extend beyond the tip of the abdomen. The intermediate forms have wings between .55 and .70 mm. I have no idea whether this polymorphism is genetic or determined by the environment. Populations predominately of long or short winged forms occur both in cold and very warm weather.

This species of scale is dispersed by the wind, probably in the crawler stage, and many isolated females must survive but can not reproduce until they are fertilized. While males will also be dispersed in the crawler stage and may develop in the same area as those females dispersed, the chances of the females being fertilized can only be increased by adult males being blown from the founding colony. The long-winged males are poor fliers but this would not necessarily be a great disadvantage because even many of the migratory insects are passively borne by the wind although they maintain altitude by flying actively (Johnson 1969). The very act of taking off would increase the chances of dispersal. The likelihood of males finding dispersed females would be increased in such areas as South Australia where there are strong prevailing winds (from the west).

Giliomee (pers. comm.) has suggested that in such sedentary insects wings may be of little importance and there may be an evolutionary trend towards aptery.

Male coccids are most commonly fully winged but in some species only apterous or brachypterous males have been described. Males of some species are dimorphic. Imms and Chatterjee (1915) found both apterous and alate males in the first generation of *Laccifer lacca* but in the second generation only apterous males were produced. Beardsley (1960) and Afifi (1968) reported apterous and macropterous forms in *Saccharicoccus sacchari* and Ghauri (1962) described males of both wing forms from *Chionaspis salicis* and *Parlatoria blanchardii*. Brachypterous and macropterous forms have been described from *Gossyparia spuria* (Afifi, 1968) and *Palmicola palmarum* (Beardsley, 1960).

Large numbers of male coccids have seldom been examined and this is almost certainly why so few dimorphic forms have been described. This seems the first report of a male with three wing forms.

There was significant variation in the mean width of the head capsule between samples of males collected at different times but in only one sample was there any relationship between wing length and size of head capsule, brachypterous males having smaller head capsules (mean and S.E. = .204 mm ± .003, n = 13) than fully winged forms (mean and S.E. = .212 mm ± .002, n = 47) ($p < .05$). These brachypterous males also had shorter bodies (mean and S.E. = .983 mm ± .049, n = 13) than the macropters (mean and S.E. = 1.122 mm ± .014, n = 47) ($p < .05$). In the other samples there was no indication that short-winged forms were smaller. Beardsley (1960) found that brachypterous males of *Palmicola palmarium* had one less antennal segment than macropterous forms. There was no such variation in the males of *E. coriaceus*, all forms having 10 antennal segments.

CHAPTER 3

Population dynamics of *E. coriaceus*

3.1 Sampling in the field

This chapter outlines the methods used to survey populations of *E. coriaceus*. The results in terms of the trends in time of the numbers of female scale, indices of population trend between successive generations, survival and causes of mortality to the female scale and the variation in the reproductive capacity of the females are examined.

Sampling consisted therefore firstly in the estimation of the numbers of female scale on each tree and secondly in estimating the survival and causes of mortality to the female scale. The methods used to estimate the numbers of scale on a tree are first described after a discussion of the populations which were sampled.

3.1A Populations sampled

Populations were studied in two areas at the Waite Institute, in the plantation near Alverstoke Orchard and in the Mallee Block (1.3). The scale typically infests one tree, or a small group of trees, in an area where there are many suitable trees which are not infested (i.e. populations are localized). Thus a census in the plantation near Alverstoke in July 1971 showed that only 7 out of 50 trees supported populations of *E. coriaceus*. Any sampling method based on the selection of twigs, or trees, purely at random was clearly not appropriate and I decided that the simplest way of sampling the populations of scale was to select number of infested trees and follow the number of female scale on each tree from generation to generation.

I will first discuss the populations which were sampled near Alverstoke Orchard. The plantation contains 6 species of eucalypts, most of which are arranged in blocks of 10. E. cladocalyx was the only species where several trees were infested and three of these (Obs. 1, Obs. 2 and Obs. 3) were chosen at random in July 1971. Another (Obs. 4) was used later.

In early September 1972 the populations of nymphs on three of the survey trees (Obs. 1, 2 and 4) were used to seed populations for a field experiment on the influence of ants on the survival of the scale (Chapter 4). I used the survey trees because two of them contained the only populations of sufficient size to seed the number of trees required for the experiment.

The populations of scale attended by ants in the experiment were under natural conditions and furnished important information on the predators and parasites active at the time. Five populations of those still in existence in November 1972 were chosen and followed until March 1973, and one other population, not included in the ant experiment but in that group of trees, was studied in January and March 1973. As the populations were artificially established the numbers of female scale they contained in November 1972 have not been included in the population survey data, but the trends in population growth on these five trees after November 1972 and up to January 1973 and the trends on the trees where there were still survivors from January to March 1973 have been used.

The populations sampled near Alverstoke were on Obs. 1, 2, 3 and 4 until August 1972 and on trees A1, A4, A6, A8, A10 and A12 between November 1972 and March 1973. Infested trees were examined in the Mallee Block and, from these, trees up to about 2.5 m high with scale were chosen at random. Populations were examined on trees 1842A, 1821C, 1954B and 1908B for various lengths of time, and on an unnumbered tree (*E. erythronema*) in March 1973.

If the population on a tree was completely wiped out then another population in the area was chosen to replace it.

3.1B Methods for an accurate estimation of the number of adult female scale in a population

The scale in very small populations were scattered or in small colonies and all could be counted i.e. the population was censused.

In most larger populations the scale occurred in compact and well defined colonies. The number of females in a colony could be calculated by measuring the area covered by the colony, estimating the density of the females in the colony and multiplying the two together. In populations of up to about 10,000 scale the number of scale in each colony was estimated as described above, single scale were counted and these were added together to give the population on the tree.

Populations larger than 10,000 individuals were usually made up of a large number of colonies and it was too time consuming to estimate the number of scale in every colony (as above). The method used was to count the number of colonies, estimate the mean number of scale per colony (from a sample) and then calculate the total number of scale on the tree.

The next section concerns the methods for measuring the area of a colony, estimating the density of the scale in the colony and sampling the large populations. The method for examining a tree to count the numbers of colonies or to census the population is outlined a little later for it is more easily described once the sampling plan for the larger populations has been explained.

3.1C The development of a sampling plan

The range in colony size (i.e. number of scale per colony) was very great for groups of 10-20 scale were commonly found and some colonies contained 1,000 individuals. The density (i.e. number of females per square centimeter) varied between colonies. Once a method for measuring areas and estimating densities had been developed it was not only possible to estimate the number of scale in populations of up to 10,000 scale but also to examine the distribution of colony size in larger populations and to develop a reasonable plan for sampling them.

The large population on tree 1842A was chosen to construct a sampling plan in November and December 1971.

3.1D The area of the colony

Twigs of many species of eucalypts are almost perfect cylinders over short distances. The diameter (D) of a twig which the scale covered was measured to the nearest .5 mm (using vernier calipers). If the colony was very long or the twig narrowed, two measurements were taken

Figure 3.1

The division of a colony into the basic sampling units.


4
3
2
1

(proximal and distal to the colony) and the mean calculated. The length of the colony (l) was measured to the nearest millimeter. The area occupied by the colony was calculated as πDl. Sometimes the cylinder so measured was not entirely covered by the bodies of the insects, in which case the actual area covered, as a fraction of the whole, was estimated by eye.

Where colonies were continuous over several twigs at a fork they were divided into sub-colonies, which were the basic sampling units used in these very large populations (Figure 3.1). To measure the total area of such an aggregate the area of each of the component parts was first measured (there are four in Figure 3.1), each sub-colony being from the fork to the limit of the colony on each of the twigs at the fork. These were the smallest sampling units available and were used in preference to the actual colonies, thereby reducing the sampling variances. The sampling unit, therefore, might be a whole colony if there was no branching, or parts of a colony when the whole colony was spread over several twigs at a fork.

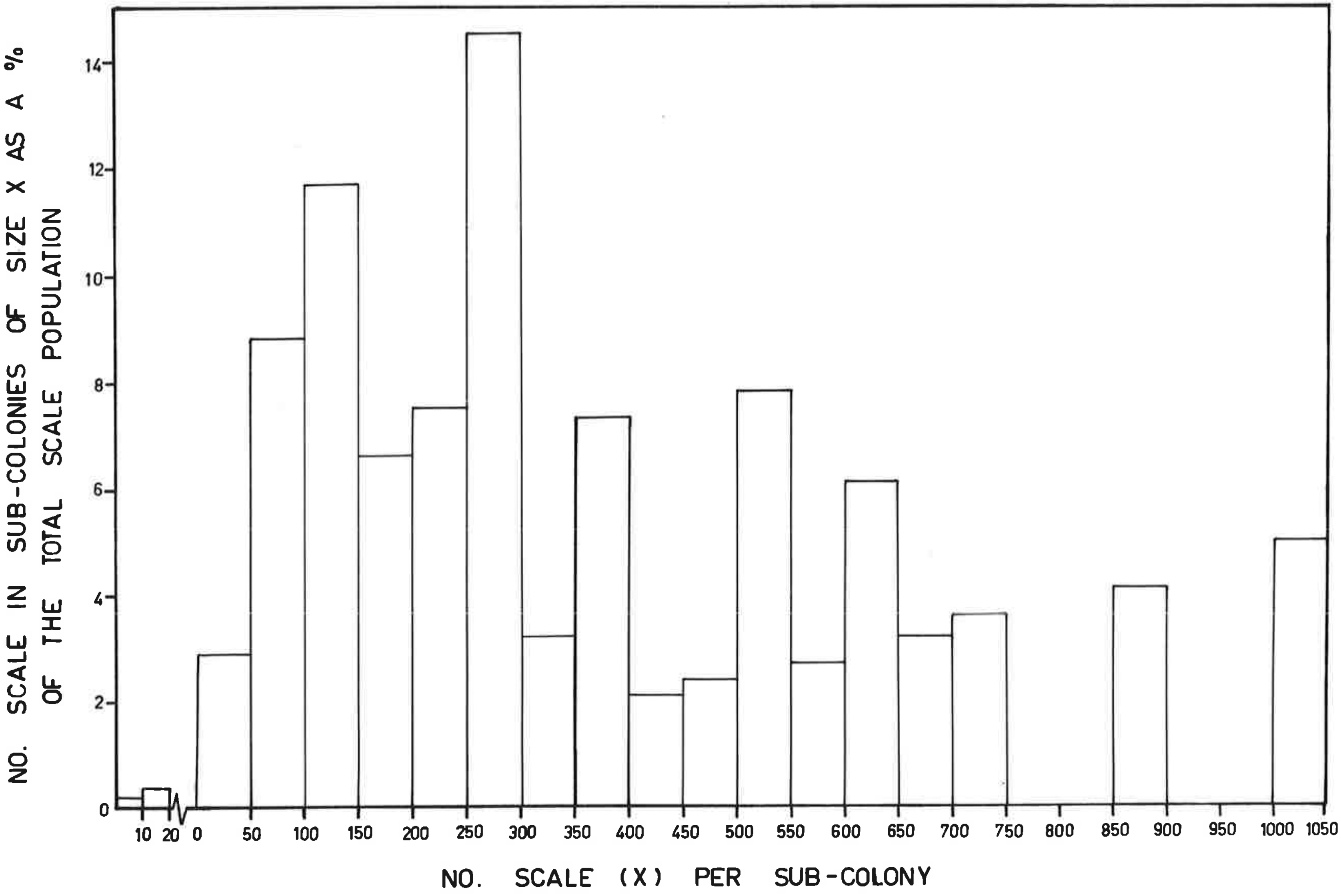
3.1E The density of the females in the colony

The next problem was to develop a technique for estimating the density of the females. A method of grading densities by eye into different categories was devised as follows:

1. Sparse. Scale an appreciable distance apart.
2. Moderately dense. Each scale separated by about one body diameter from its neighbours.

Figure 3.2

The relationship between the number of individuals in a sampling unit and the percentage of the total population contained in units of that size.


NO. SCALE IN SUB-COLONIES OF SIZE X AS A %
OF THE TOTAL SCALE POPULATION
0
2
4
6
8
10
12
14
10
20
0
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
900
950
1000
1050
NO. SCALE (X) PER SUB-COLONY

3. Dense. Most scale closely packed but usually not touching their neighbours on all sides. The scale in this category are not deformed by crowding.
4. Very dense. Most scale touching their neighbours on all sides, some deformed by close contact.

In order to quantify these density categories, thirty sampling units were selected and examined. Each was placed in one of the four categories. Then the area of each was measured and the number of scale it contained counted. Where the scale were very dense it was necessary to mark each (with a spot of water soluble ink applied with a fine brush) as it was counted. The density of the scale in each sampling unit was calculated.

In 15 units the scale were judged by eye as very dense (mean density was calculated as 24.5 scale cm^{-2}, range 15.1 - 32.0); in 9 dense (14.9, 11.1 - 18.5); in 4 moderately dense (7.0, 5.6 - 10.5) and in 2 sparse (3.5 scale cm^{-2}). Although there was some slight overlap these basic categories were subsequently used.

3.1F The size distribution of the basic sampling units

The number of scale in every large sampling unit on the tree was estimated, and isolated or small groups of scale were counted. Figure 3.2 shows the relationship between the number of individuals in a sampling unit and the percentage of the total population which units of that size contributed. Those with under 20 individuals contributed only .6% of the total population. Thus these small colonies, which were

Figure 3.3

The relationship between length of sub-colony (sampling unit) and the mean number of scale contained in sampling units that length.

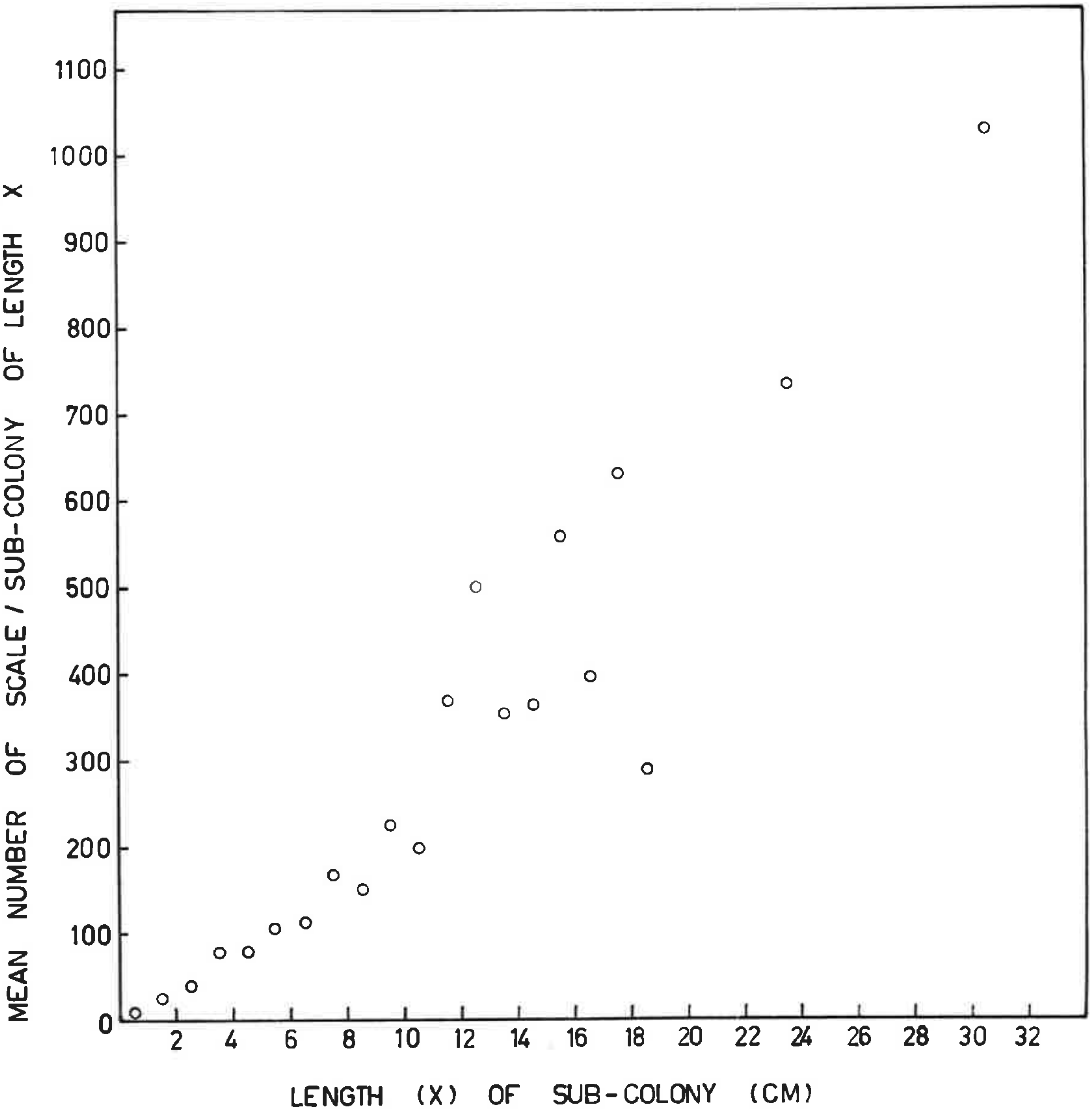

MEAN NUMBER OF SCALE / SUB-COLONY OF LENGTH X
0
100
200
300
400
500
600
700
800
900
1000
1100
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
LENGTH (X) OF SUB-COLONY (CM)

Figure 3.4

Frequency distribution of sub-colonies (sampling units) of different lengths. The arrow shows the length, 10 cm, used as a basis for dividing colonies into large and small.

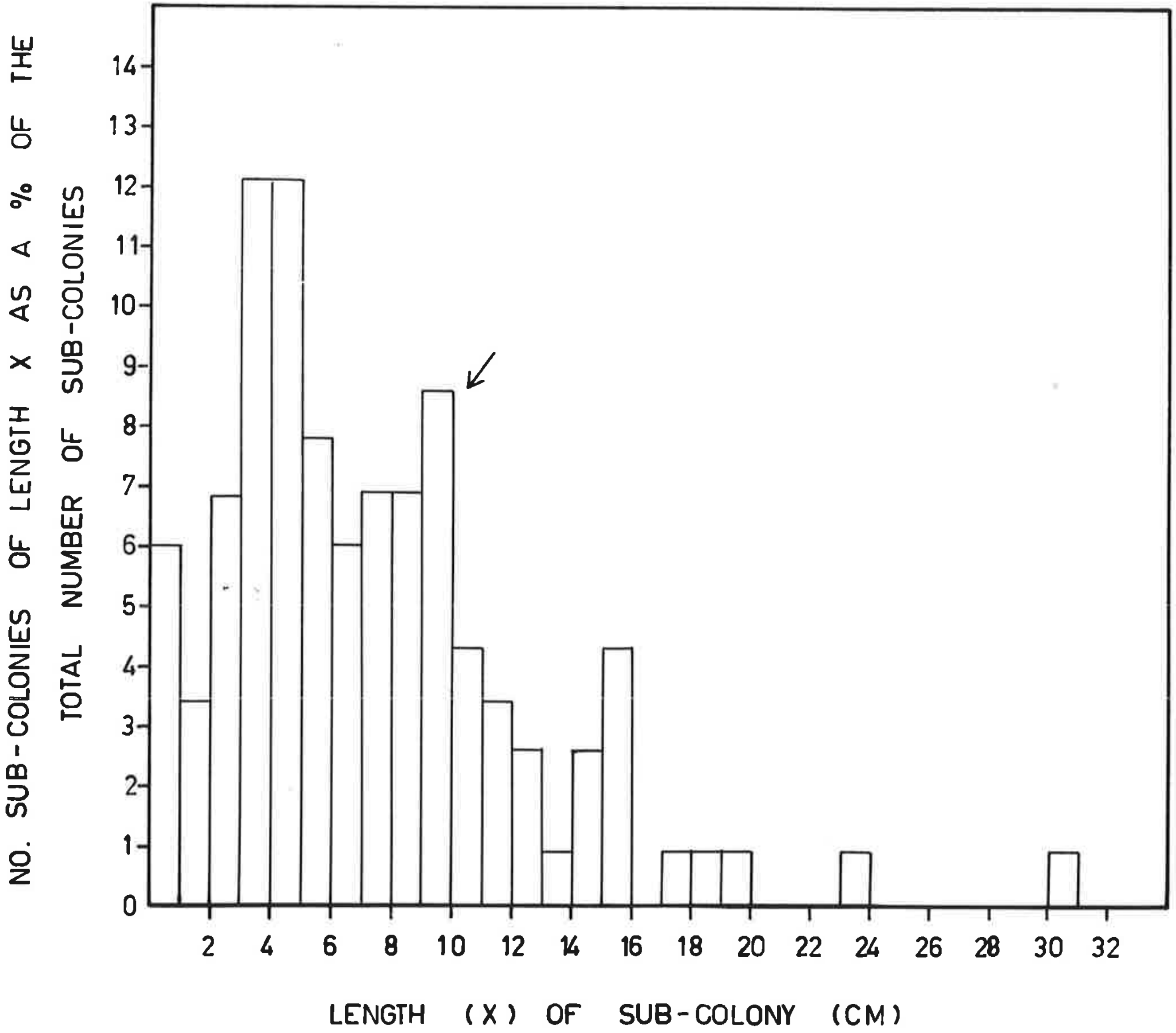
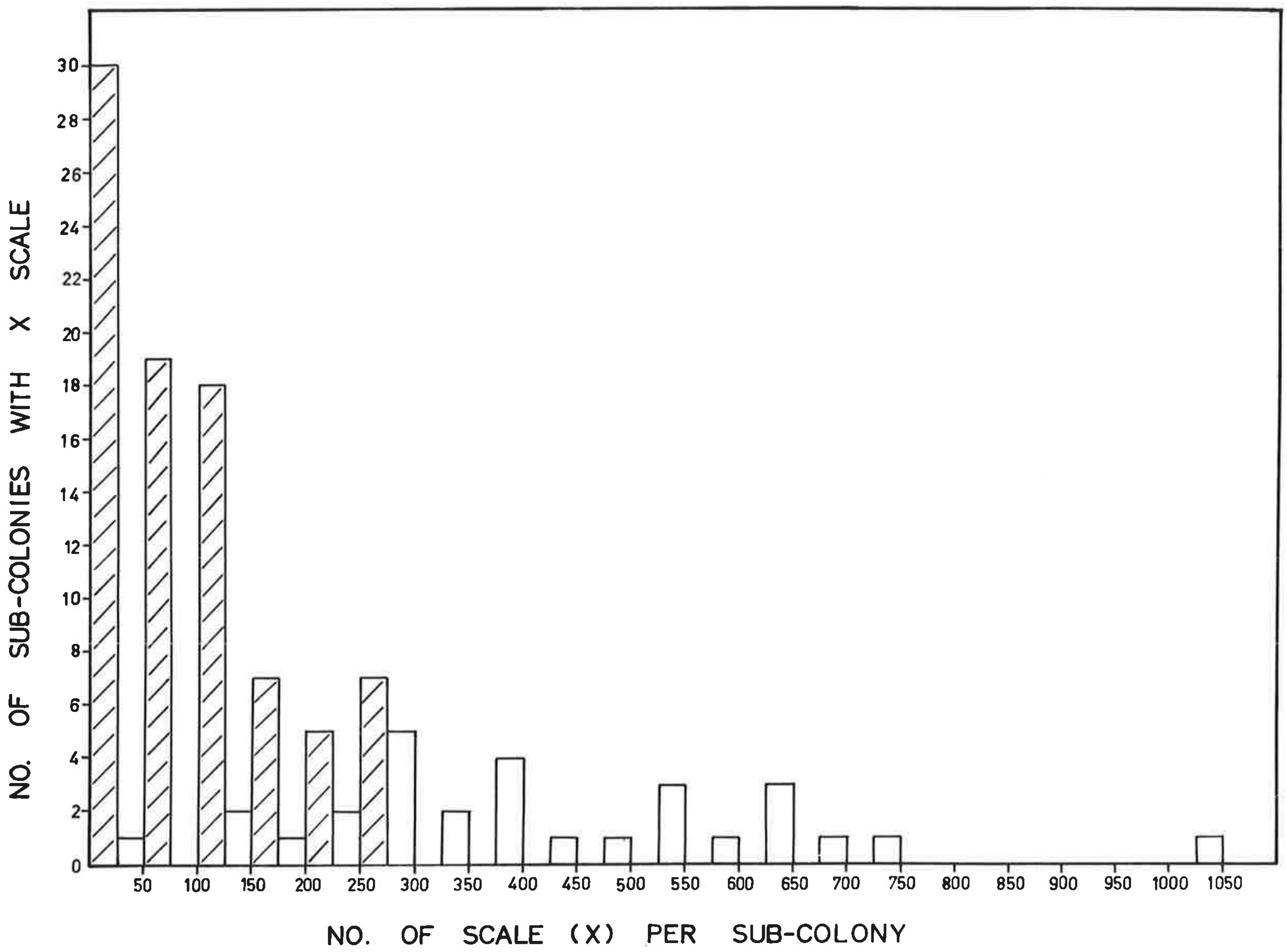

NO. SUB-COLONIES OF LENGTH X AS A % OF THE TOTAL NUMBER OF SUB-COLONIES
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
LENGTH (X) OF SUB-COLONY (CM)

Figure 3.5

This figure shows the division into small (hatched) and large (open) colonies using length (10 cm) alone as a dividing line. There is considerable overlap. When other criteria are applied all but one of the large colonies containing below 250 individuals are then relegated to the class of smaller colonies.


NO. OF SUB-COLONIES WITH X SCALE
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
50
100
150
200
250
300
350
400
450
500
550
600
650
700
750
800
850
900
950
1000
1050
NO. OF SCALE (X) PER SUB-COLONY

sometimes difficult to find, were ignored in these very large populations without introducing any appreciable error into the estimate of the total number of scale on the tree.

A plan to sample the larger units was then devised. Because of the large range in the numbers in the basic sampling unit the method of Cochran (1939) was used and the sampling units were divided into clases, i.e. stratified. The simplest method was to divide them into large and small. To do this some easily recognizable criterion of size (i.e. the number of individuals in the sampling unit) was needed.

As mentioned previously the number of scale in a sampling unit depends on:

a. The length of the unit.

b. The diameter of the twig.

c. The density of the scale.

d. The proportion of the twig covered by scale.

The area was calculated as ΠDl. The diameter varied from .15 to 1.5 cm whereas the length varied from 1 to over 30 cm; length was thus the major factor contributing to the variation between sampling units. When the number of scale per sampling unit was plotted against the length of the unit (diameter, density and coverage being neglected) it was apparent that the number was closely related to length (Figure 3.3).

The relationship between sampling units of various lengths and the percentage of the total number of units contained in those classes is shown in Figure 3.4. The population of sampling units was divided so there would be minimum likelihood of the classes overlapping. If Figure

3.4 is examined, a natural break occurs at 10 cm. There were many sampling units in all classes until the 10.1 - 11.0 cm class which contained only half as many as the previous class. 86 of the 116 sampling units (74.1%) fell below this class length. There were relatively few larger sampling units. The likelihood of confusing small and large units would thus be least if 10 cm were used as a dividing line. The two classes of sampling units so formed contained approximately equal proportions of the total number of scale on the tree (43.9% and 56.1%).

When the population of sampling units was divided according to length alone, and for each of the two classes so formed the number of units containing 0-50, 51-100 etc. individuals was plotted against the length of the sampling unit (Figure 3.5) there was still considerable overlap. This was because the effect of density and the proportion of the cylinder (delineated by the gross dimensions of the unit) covered by scale, had so far been neglected.

Of the 86 smaller units, 49 were classed as very dense, 19 as dense, 4 as moderately dense and 14 as sparse. Of the 30 larger units, 26 were very dense, 3 dense and one was sparse. Sparse and moderately dense sampling units classed as large on length alone, were relegated to the class of small units. In five of the 30 sampling units the area of the cylinder was less than half covered by the bodies of the insects. An arbitrary decision was, therefore, made and units 10 cm long or just above 10 cm, dense or very dense but less than half covered with scale were classed as small. Any further delineation was too cumbersome to be applied in the field. When these criteria were applied to the sampling units under consideration the overlap between classes was greatly reduced, all but one colony with below 250 scale being relegated to the class of smaller colonies. There were thus 91 smaller sampling units and 25 large sampling units. The next step was to estimate the mean size of each class and then the total population on the tree could be calculated.

There were, however, in the 91 units, 11 colonies which had below 20 individuals; since these formed a negligible proportion of the total population they were ignored (see above) and do not enter the sampling estimations.

There were thus 80 small sampling units and 25 large sampling units.

3.1G The estimation of sample size for a certain error

The number of sampling units, n, that have to be drawn at random from a population of N units to produce an estimate of the mean within a certain agreed-upon error, d, depends on the variance of the population and the risk, α, we are willing to accept that the actual error is larger than d.

The required level of accuracy (i.e. the value of d) is usually 10% (Southwood, 1966, page 19). From the initial observations on *E. coriaceus* it seemed likely that very large changes in population could be expected and therefore the margin of error for these populations was chosen as 30%. (It should be remembered that in the overall study most populations were below 10,000 and were sampled by estimating the number of scale in each colony and the accuracy is therefore likely to be much better than

± 30%).

$$n = \frac{t^2 s^2}{d^2} \;/\; 1 + \frac{1}{N}\frac{(t^2 s^2)}{d^2}$$ (Snedecor and Cochran, 1968)

where n number of units required for 30% accuracy

y sample mean

s^2 sample variance

d desired margin of error $.3y$

t abscissa for the normal curve cutting off an area at the tails ($t = 2$ for $\alpha = 2.5\%$).

N the number of units in the population.

The total number of sampling units in each stratum, (N), was counted and from these, five units (in each stratum) were selected at random. The variance and mean, and the desired margin of error, d, were found for each sample of 5 units. The required number of sampling units in each stratum was then estimated as follows:

For the class of larger units $N = 25$

$s^2 = 33538.70$

$y = 392.2$

$d = 117.7$

n is 6.98. That is, to achieve the desired accuracy, 7 large colonies must be sampled. Since 5 had already been chosen for the above data, two more were chosen and the mean was recalculated as 378.9.

For the class of smaller colonies $N = 80$

$s^2 = 6546.30$

$y = 128.4$

$d = 38.5$

n is 14.5. That is, to achieve the desired accuracy, 15 smaller colonies must be sampled. So, since 5 had already been chosen, ten more were chosen and the mean recalculated as 105.0.

As a result of the above sampling procedures the total number of scale on the tree was consequently estimated to be:

In large colonies	9473
In small colonies	8400
Total	17873

This estimate was then compared with the more accurate estimate derived from the total of the sampling units, which was 20,730.

The percentage error is $\frac{2857 \times 100}{20730} = 13.78\%$

If the method of stratified sampling is compared with simple random sampling the advantages become apparent. In order to achieve an estimate of the same accuracy by taking units at random from the whole population of 105 sampling units, a sample size of 35 would be needed (compared with only 22 using the stratified method).

$$N = 105$$

$$s^2 = 35309$$

$$y = 169.6$$

$$d = 50.88$$

(Ten samples were used to calculate variance and mean).

$$n = 34.95$$

Sampling data for all populations on which this method was used are given in Table 7 appendix.

3.1H The inspection of the tree

So far I have not mentioned how I examined the tree to determine the population on it. I examined the tree in a systematic manner to ensure that I missed as few scale as possible. It was almost immediately apparent whether the scale population was below 10,000 or very large. If the population was below 10,000 I started from the base of the tree and worked in a clockwise fashion from branch to branch (and from the base to the tip of the branches), counting the scale or estimating the areas and densities of the colonies as I went. If the population was very large I worked in the same manner and examined all sampling units, placing them in either the large or small category. Any borderline cases were measured and the criteria already discussed were applied. Once the total number of colonies in each class had been obtained, five were selected at random from each category and the colonies were re-located by counting in the same manner as before. The area of the colony was measured and the number of scale estimated. The mean, variance and number of samples needed in each category were calculated and further samples taken if necessary.

3.1I Further comments on the estimation of the density of colonies

The necessity for estimating the densities of the colonies and its importance in sampling has already been discussed. There were two aspects to the measurement of colony density. Firstly I had to check the accuracy of my visual estimation of colony density and secondly it was apparent, after some time, that the mean density of the colonies varied with the season (see 2.2D).

On each tree sampled, a small number of colonies was selected (often those used for estimating mortality), the densities of the colonies were first estimated by eye (i.e. placed into one of the density categories) and then measured accurately as described previously. This enabled a check on the visual approximation, and also gave an estimate of the mean density of scale on that tree at the time.

For the purpose of estimating the number of scale in a colony the initial density categories were usually sufficient, but if the scale in the most crowded colonies had a mean density greater than 24.5 scale cm^{-2} then a new density category was erected for these colonies using the actual mean calculated for them.

In late summer the density of colonies was about 2-3 times that for the rest of the year. The colony lengths were usually shorter at this time and on those trees with populations in excess of 10,000 scale the dividing line between the classes of large and small sampling units was arbitrarily reduced to 5 cm.

3.1J Sampling for populations of scale on leaves

In the winter of 1972 three trees had populations of scale not only in colonies on the twigs but also widely dispersed, in small numbers, on the leaves. On two of these trees (1842A and Obs. 4) the number of leaves infested was below 500. The number of infested leaves was determined by a census. The mean number of scale per leaf was estimated from a random sample of infested leaves. Sampling data for these trees are given in the appendix (Table 8).

One tree (Obs. 1) had such a large number of scale on the leaves that some sampling procedure was necessary to determine the number of leaves infested. This method is described in the footnote to Table 8 in the appendix.

Where scale occurred both on the leaves and on the stem each stratum was sampled separately to determine percentage survival and causes of mortality. An estimate for the whole population was then made by weighting these percentages with the proportion of the total population that occurred in that stratum. A similar procedure was followed where small and large colonies were sampled on trees with large populations in the ant experiment.

3.1K The timing of sampling to determine survival of females and causes of mortality

The methods for the removal of a sample have been described in 1.6B. Comments here concern the timing of sampling.

Although the number of scale on a tree could be estimated without destructive sampling it was necessary to remove a sample from the population to measure the length of the female scale and to examine the females to determine the proportion of survivors and causes of mortality. Although on some trees scale were numerous, on others the population was quite small and could only be sampled once without removing a very large proportion of the total population. I decided to remove the females when areas of crawlers were produced i.e. soon after the beginning of reproduction. This was the obvious time to measure the survival rates of the females for reproduction was often synchronous within a population and the reproductive period was relatively short. Thus the proportion of females alive at this time would have been approximately the proportion which had produced most of their young. The timing of sampling was important and whilst the sampling of the populations near Alverstoke was straight forward it was more difficult in the Mallee Block.

The populations near Alverstoke were sampled on about the dates given in 2.2F. The populations in the Mallee Block were sampled in November 1971, between January and April 1972, August 1972, November 1972 and January and March 1973. Between January and March 1972 the populations on 1908B and 1821C overlapped and the populations on 1842A and 1954B were very small. Each population was sampled once in January or February and once in March or April when I considered most females were mature and young were being produced. The data for January and February have been considered together as have the data for March and April. The populations were all sampled in mid August and November 1972.

This timing was satisfactory for populations on 1842A and 1954B but on both occasions many females on 1908B had reproduced prior to sampling. During the summer of 1973 few young were produced and the populations were sampled in January and March 1973. Observations were made in February 1973 (e.g. on 1954B) but no samples were taken.

While the mistiming of sampling influenced the estimation of female survival (a comment on this is made later) it had relatively little influence on the estimation of the causes of mortality. The scale bore the marks of the predators or parasites which had quite clear cut seasonal patterns of occurrence, hymenoptera being virtually absent in the cooler months and *R. ventralis* being absent in summer.

3.2 Trends in the numbers of female scale

The stage chosen to sample for an estimate of abundance is important. Morris (1963) recommended the use of the egg as this was qualitatively the least variable stage. I have used the number of female scale which settled and secreted tests as an estimate of abundance for this is the stage most easily sampled. Furthermore the newly settled female is valuable to the population, for she often has a good chance of reproducing i.e. her reproductive value (Fisher, 1958) is high, whereas a crawler has a very small chance of surviving and has a very low reproductive value.

I have examined both the numbers of scale present in the populations in each generation and the indices of population trend between the same population in successive generations. The number of scale in a population is obviously important but so too are the trends of the populations, for an erratic increase or decrease in one large population may hide an overall trend in the opposite direction by many smaller populations. In an organism such as *E. coriaceus* with very limited powers of dispersal the trends in individual populations may be more important than actual numbers in an area i.e. it may be more important that many small populations increase slightly (or for that matter even continue) than that one large population is greatly reduced or increases greatly. This is

TABLE 3.1 Data for survey trees near Alverstoke Orchard (Waite Agricultural Research Institute) showing populations of female *E. coriaceus* on trees at different times of sampling and the logarithm (population + 1).

Tree No.	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Obs. 1	191	14,905	21,570	41,520	23,382			
2	565	30,174	1,084	818	294			
3	46	764	0	-	-			
4	-	-	10,104	14,136	6,103			
Trees seeded experimentally in September 1972								
A1						362	29	0
A4						96	24	0
A6						1,147	10,892	0
A8						705	17	0
A10						1,384	221(124)	458
A12						-	423(331)	1,234
Obs. 1	2.2833	4.1735	4.3339	4.6182	4.3689			
2	2.7528	4.4796	3.0350	2.9133	2.4698			
3	1.6721	2.8837	0	-	-			
4	-	-	4.0047	4.1511	3.7856			
A1						Not included in analysis of population numbers as they were artifically seeded.	1.4771	0
A4							1.3979	0
A6							4.0334	0
A8							1.2553	0
A10							2.3444	2.6618
A12							2.6274	3.0917

TABLE 3.2 Data for survey trees in the Mallee Block (Waite Agricultural Research Institute) showing populations of female *E. coriaceus* on trees at different times of sampling and the logarithm (population + 1).

Tree	August 1971	November 1971	January-February 1972	March April 1972	August 1972	November 1972	January 1973	March 1973
Population								
1842A	1,492	20,730	258(205)	1,350	4,455	1,860	130	33
1954B	-	-	146(96)	81(53)	167(120)	2,096	230	0
1908B	-	-	8,374	1,622	324(257)	355(234)	394(244)	25
1821C	-	1,392	21	0	-	-	-	-
Log. (Population + 1)								
1842A	3.1738	4.3166	2.4116	3.1303	3.6489	3.2695	2.1139	1.5185
1954B	-	-	2.1644	1.9085	2.2227	3.3214	2.3617	0
1908B	-	-	3.9229	3.2100	2.5105	2.5502	2.5955	1.3979
1821C	-	-	1.3222	0	-	-	-	-

probably not so for most insects which have a highly dispersive adult stage which can move out from an area of high larval density and lay eggs over a large area.

The index of population trend is defined as $I = \frac{P(n+1)}{Pn}$ where P = total population of a given stage and n = any generation (Southwood, 1966, page 295).

Notes. Female scale were removed soon after the beginning of reproduction for an estimation of mortality (1.6B). On most trees these did not constitute a significant proportion of the total population but on some trees in both the Mallee Block and near Alverstoke Orchard (January 1973) the scale removed reduced the population significantly. The number of female scale on the tree before and after sampling are shown, the latter figures being in brackets in Tables 3.1 and 3.2. For these trees the indices of population trend are based on the numbers after sampling in one generation and the total population in the next generation. This is clearly an approximation because many young had been produced by the time the females were removed. In fact these corrections make little difference to the trends. In some very small populations, especially in January 1973 in both areas, females were examined on the trees as the removal of a sample of the very few survivors would have seriously endangered the populations.

3.2A Analysis of numbers of females. August 1971 - March 1973

The number of females in each population sampled and the log (number + 1) for each population is given in Tables 3.1 and 3.2. There was significant variation between the means of the transformed numbers in the populations (log(number + 1)) at the different times of sampling ($F_{7,43} = 3.861$; $p < .05$).

The arithmetic means for the numbers of female scale at different sampling times and the mean log (number + 1).

Date of sampling	Mean log (pop. + 1)*	Arithmetic mean of population
August 1971	2.4706	574
November 1971	3.7995	13,593
January-February 1972	2.6531	5,195
March-April 1972	2.8482	8,504
August 1972	3.1751	5,788
November 1972	3.0472	1,001
January 1973	2.2459	1,373
March 1973	.9667	194

* Significant differences (determined by using the method of least significant difference) marked.

Populations were very small in March 1973 (arithmetic mean 194) and the mean log (number of scale per tree + 1) differs significantly from that at any other time. The only other significant difference was that between the transformed data for the large populations in November 1971

TABLE 3.3(a) Data for survey trees near Alverstoke Orchard showing indices of population trend between successive populations of female *E. coriaceus*.

Tree	August to November 1971	November 1971 to January 1972	January to March 1972	March to August 1972	August to November 1972	November 1972 to January 1973	January to March 1973
Obs. 1	78.037	1.447	1.925	.563			
Obs. 2	53.405	.036	.755	.359			
Obs. 3	16.609	0	-	-			
Obs. 4	-	-	1.399	.432			
Trees seeded experimentally in September 1972							
A1					-	.081	0
A4					-	.250	0
A6					-	9.946	0
A8					-	.024	0
A10					-	.164	3.694
A12					-	-	3.728

TABLE 3.3(b) Data for survey trees in the Mallee Block showing indices of population trend between successive populations of female *E. coriaceus*.

Tree Trend Index	August to November 1971	November 1971 to January 1972	January to March 1972	March to August 1972	August to November 1972	November 1972 to January 1973	January to March 1973
1842A	13.894	.013	5.233	3.030	.418	.070	.254
1954B	-	-	.844	2.062	12.551	.092	0
1908B	-	-	.194	.200	1.096	1.110	.063
1821C	-	.015	0	-	-	-	-

and the small populations in January 1973 (arithmetic means 13,593 and 1373 respectively). Although the (arithmetic) mean number of scale per tree increased from 574 in August 1971 to 13,593 in November 1971, the variation in the number of scale per tree was so great that there was not a significant difference, using the transformed data, between these two sampling periods. Use of the indices of population trend, however, indicated that this was a time of increasing populations (see next section).

Despite the lack of more significant variation between sampling times, it seemed likely that the female scale which settled in the cooler months and reproduced in August and November were more numerous than those which settled in December to March and reproduced from January to early April. Thus if log (number of scale per tree + 1) of those populations reproducing in August and November were pooled for both years and compared with log (number of scale per tree + 1) of those populations reproducing between January and April of both years the former are significantly greater (means 3.1707 and 2.1235 respectively, $t = 4.959$, 49d.f., $p < .005$. Arithmetic means 6,072 and 3,389). Even if the data for March 1973 is considered aberrant and is excluded the trend of larger values for log (number of scale per tree + 1) for the populations reproducing in August and November is still maintained (means 3.1707 and 2.5573 respectively, $t = 3.440$, 40d.f., $p < .005$. Arithmetic means 6,072 and 5,413).

3.2B <u>Analysis of indices of population trend. August 1971 - March 1973</u>

The indices of population trend are shown in Tables 3.3(a) and

3.3(b). Only the great increasing trend from August to November 1971 differed significantly from all others ($F_{6,35} = 10.525$; $p < .005$). Not only were the populations at any time highly variable, but the trends between successive populations over any one period of time were also highly variable.

Seasonal variation in mean trend index

Period	Mean trend index
August to November 1971	40.486
November 1971 to January 1972	0.302
January to March 1972	1.479
March to August 1972	1.108
August to November 1972	4.688
November 1972 to January 1973	1.467
January to March 1973	0.967

Four of the five populations which increased from August to November 1971 collapsed between November 1971 and January 1972, three having indices below .05 and one being completely wiped out. From January 1972 to March 1972 trends were variable and no pattern was detectable, three populations increasing and three decreasing (mean index 1.48). From March 1972 to August 1972 two populations increased and four decreased but overall the mean trend index was stable at 1.108. From August 1972 to November 1972 only three populations were studied; one of these showed an increase (12.551 fold) of similar magnitude to that of the four populations the year before, one was stable (1.096) and one declined (.418).

The trends from November 1972 to January 1973 were similar to those of the same period in the previous year. Six of the eight populations studied decreased markedly, one population was stable and one increased nearly 10 fold. The populations which decreased between November and January had very low trend indices, those in the first season (1971-1972) all being below .05, and those in the second season (1972-1973) being .024, .070, .081, .092, .164 and .250. These are generally below those for populations which decreased from March 1972 to August 1972 (.200, .359, .432 and .563).

From January 1973 to March 1973 there was a substantial reduction in population size. As four of the five populations which were originally used in the ant experiment were extinguished in January and February 1973, another population, on tree A12, was followed from January 1973 to March 1973. By March 1973 four of the six populations being studied near Alverstoke had been completely destroyed and all three of the populations in the Mallee Block declined (one of these also being extinguished). Two populations near Alverstoke showed increasing trends (3.694 and 3.728).

The data, both for populations and trend indices are highly variable. Despite this variability there was a trend for higher populations to occur in the cooler months, especially in November, and populations in summer to be low. Froggatt (1921) comments on a similar trend in the eastern states of Australia where he found the scale most abundant in October and November. A striking feature of the data was the marked decline in most populations from November to January in both years.

Figure 3.6

Data for populations near Alverstoke showing:

(a) survival of the female scale

(b) percentage of female scale killed by coccinellids (chiefly *R. ventralis*)

(c) percentage of female scale parasitized by hymenoptera

Note.

● denotes values for each population sampled

○ denotes mean where all values are shown

× denotes mean where some individual values very close to the mean or to other values have not been shown for the sake of clarity

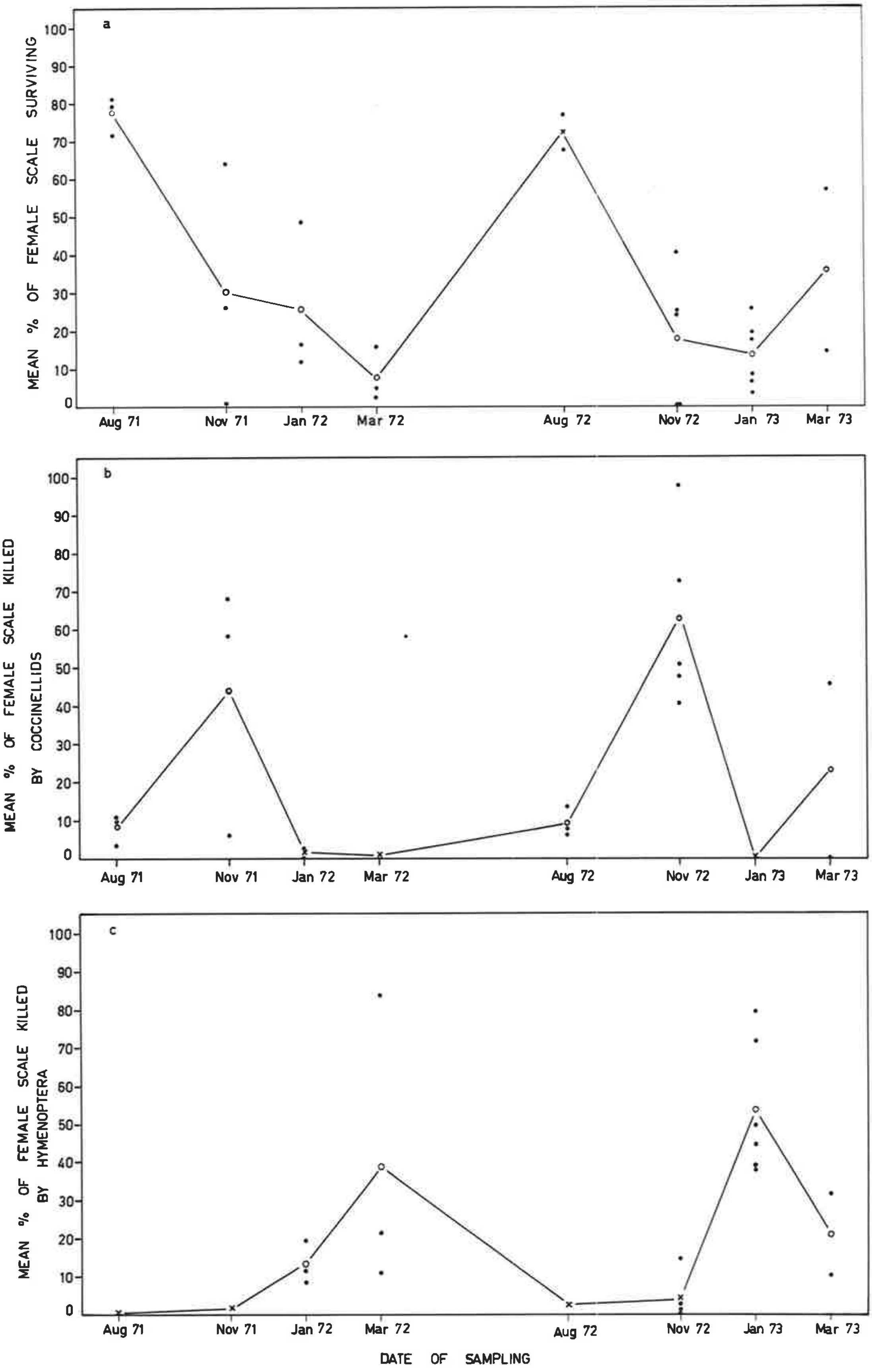

a
MEAN % OF FEMALE SCALE SURVIVING
0
10
20
30
40
50
60
70
80
90
100
Aug 71
Nov 71
Jan 72
Mar 72
Aug 72
Nov 72
Jan 73
Mar 73
b
MEAN % OF FEMALE SCALE KILLED BY COCCINELLIDS
0
10
20
30
40
50
60
70
80
90
100
Aug 71
Nov 71
Jan 72
Mar 72
Aug 72
Nov 72
Jan 73
Mar 73
c
MEAN % OF FEMALE SCALE KILLED BY HYMENOPTERA
0
10
20
30
40
50
60
70
80
90
100
Aug 71
Nov 71
Jan 72
Mar 72
Aug 72
Nov 72
Jan 73
Mar 73
DATE OF SAMPLING

Figure 3.7

Data for populations in the Mallee Block showing:

(a) survival of the female scale

(b) percentage of female scale killed by coccinellids (chiefly R. ventralis).

(c) percentage of female scale parasitized by hymenoptera

Note.

● denotes values for each population sampled

○ denotes mean where all values are shown

× denotes mean where some individual values very close to the mean or to other values have not been shown for the sake of clarity.

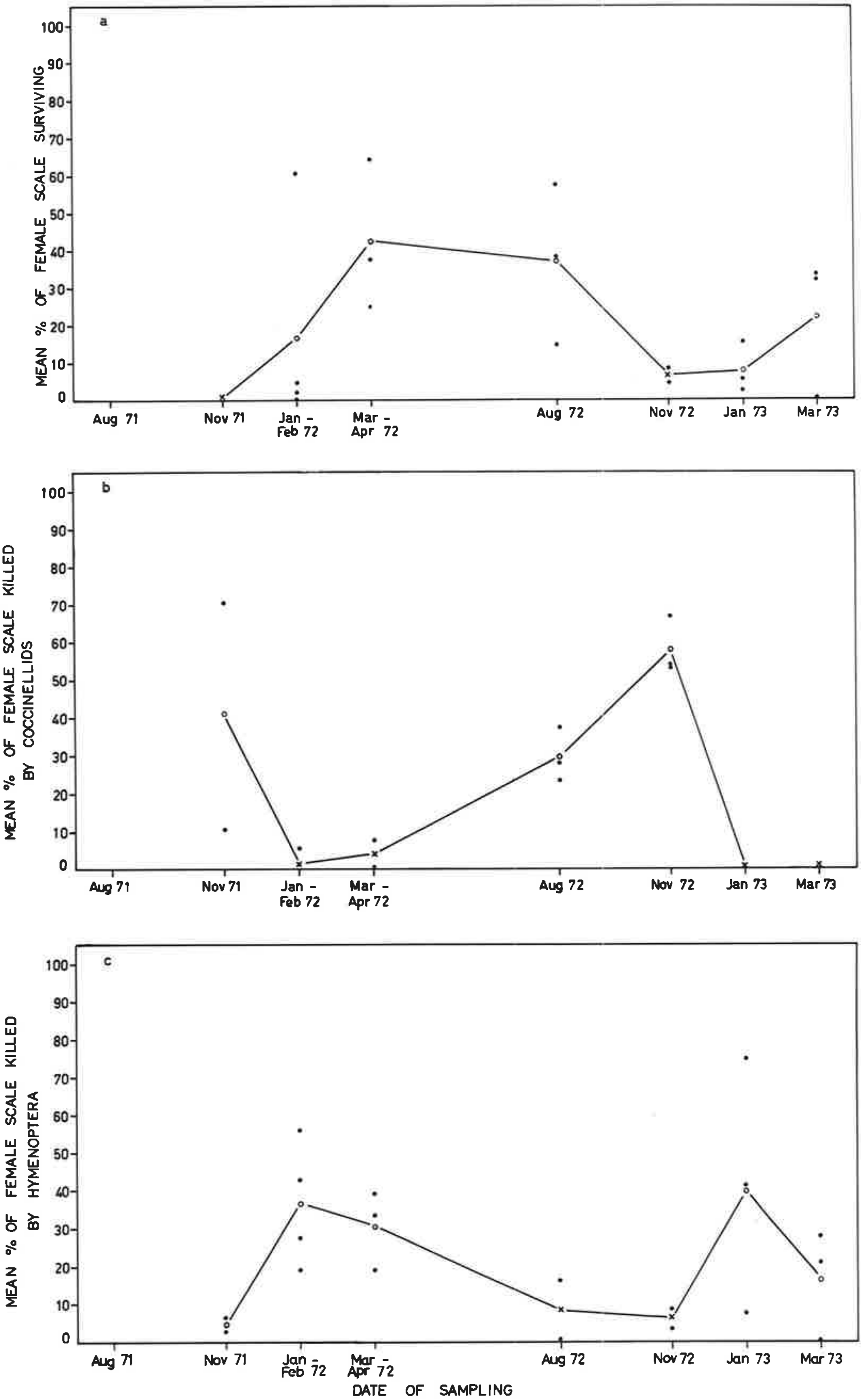
a
MEAN % OF FEMALE SCALE SURVIVING
100
90
80
70
60
50
40
30
20
10
0
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
b
MEAN % OF FEMALE SCALE KILLED BY COCCINELLIDS
100
90
80
70
60
50
40
30
20
10
0
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
c
MEAN % OF FEMALE SCALE KILLED BY HYMENOPTERA
100
90
80
70
60
50
40
30
20
10
0
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
DATE OF SAMPLING

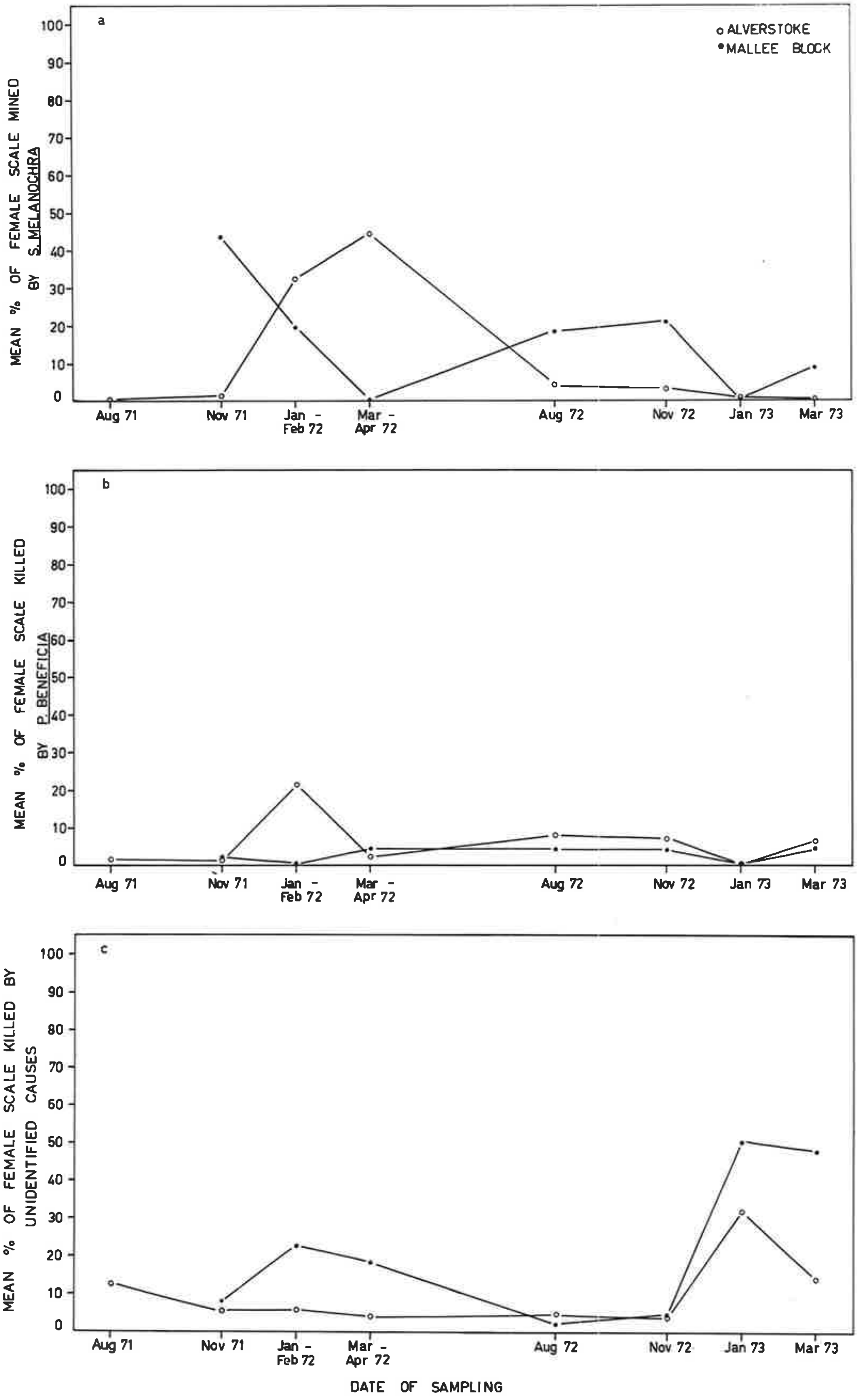
Figure 3.8

Data from populations sampled in both the area near Alverstoke and in the Mallee Block showing:

(a) mean percentage of female scale mined by S. melanochra.

(b) mean percentage of female scale killed by P. beneficia.

(c) mean percentage of female scale that were killed by causes that could not be determined.


a
o ALVERSTOKE
• MALLEE BLOCK
MEAN % OF FEMALE SCALE MINED BY S. MELANOCHRA
100
90
80
70
60
50
40
30
20
10
0
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
b
MEAN % OF FEMALE SCALE KILLED BY P. BENEFICIA
100
90
80
70
60
50
40
30
20
10
0
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
c
MEAN % OF FEMALE SCALE KILLED BY UNIDENTIFIED CAUSES
100
90
80
70
60
50
40
30
20
10
0
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
DATE OF SAMPLING

Possible reasons for this decline in numbers in the transition from spring to summer are now discussed.

Populations decrease when the death rate exceeds the birth rate and this normally occurs when mortality increases, although it can also be caused by a decrease in fecundity. The seasonal trends in the survival of the female scale, the causes of mortality to the female scale and the seasonal variation in their fecundity are examined.

3.3 Survival of the female scale and the causes of mortality

3.3A Trends in the survival of the female scale at the time of reproduction

There are obvious differences in the survival rates in the two study areas (Figures 3.6(a) and 3.7(a). Data in Table 9 appendix).

In the area near Alverstoke at the end of winter in both 1971 and 1972 survival rates were high and showed little variation. In August 1971 the mean percentage survival was 77.5% (range 71.7 to 81.2%) and in August 1972 it was 72.0% (range 67.4 to 76.6%). In both years the survival rate in November was lower than that in August; November 1971 mean 30.0% (0 to 64.0%), November 1972 mean 17.9 (0 to 40.1%). In 1972 the survival rate increased from March (7.7%, range 2.2 to 15.9%) to August (see above). Survival in January was low in both years with 25.4% (11.5 to 48.5%)of the females reproducing in 1972 and 13.6% (0 to 25.8%) in 1973. The pattern here is one of high survival at the end of winter followed by considerably lower survival rates in spring, summer and early autumn.

Survival rates in the populations in the Mallee Block were highly variable. The survival rate in early April 1972 (mean 42.3%, range 25.0 to 64.1%) was much higher than that for March in the area near Alverstoke. The reason for this discrepancy seems to be that the predator Stathmopoda melanochra was almost entirely absent from the populations in the Mallee Block whereas 44.5% (range 13.4 to 76.6%) of the females near Alverstoke were mined. Survival rates in August 1972 in this area were also relatively high with a mean survival rate of 36.9% (range 14.9 to 57.7%). Females on 1908B were removed in August but had reproduced before hand and this no doubt explains the low percentage survival (14.9%).

The trends in survival in the populations near Alverstoke are clear with a large proportion of the female scale alive at the end of winter and much lower survival rates in summer. In the Mallee Block survival rates are more variable but in both areas survival of the females at the end of winter was relatively high.

3.3B Causes of mortality to the female scale

When conditions are favourable few females die between the time they settle and begin to secrete their tests, and the time they reproduce (2.2F). Most females which die in the field are therefore killed by unfavourable conditions or natural enemies, the latter being especially important.

Rainfall and storms may kill nymphs (2.3B) but have virtually no impact on the adult females. The maximum mortality inflicted by storms on the female scale was 4% in October 1971. Death was caused by the wind whipping leaves across the newly settled females which had not completed secretion of their test. The females are very small in late summer when they exhibit reproductive abnormalities (3.4). Almost certainly some are killed by high temperatures but the extent of such mortality is unknown.

There were several other minor causes of mortality to the female scale. In one large population dense colonies were formed and some females were killed by being constricted by their neighbours, but this was not common. In late winter the dorsal part of the test of some females broke away and the actual body of the female scale fell from the tree. Some leaves with extensive colonies of female scale showed premature senescence and fell from the tree causing the death of the scale. On several occasions twigs carrying a heavy scale population died. None of these causes killed more than 5% of the female scale.

3.3C The natural enemies

The major natural enemies are listed below. Each is discussed in more detail in Chapter 5 where the less important predators are also mentioned.

COLEOPTERA:	
COCCINELLIDAE:	*Rhizobius ventralis*
HYMENOPTERA:	
ENCYRTIDAE	*Aphycopsis* spp.
LEPIDOPTERA:	
STATHMOPODIDAE:	*Stathmopoda melanochra*
NOCTUIDAE	*Catoblemma dubia*

DIPTERA:	
CHAMAEMYIIDAE:	*Pseudoleucopis beneficia*
NEUROPTERA:	
CHRYSOPIDAE:	*Chrysopa ramburi*

The action of the natural enemies may, in most cases, be identified by the characteristic way they destroy the test of the female scale (see Chapter 5). There were some difficulties in measuring the exact impact of certain predators but the method of examining the tests of the females was by far the best way to assess the influence of the natural enemies. The larvae of *S. melanochra* not only destroyed living scale but also tunnelled through the tests of the dead females. The extent of primary mortality caused by these larvae was therefore less than that which is indicated. In some circumstances this difference would have been considerable but there was no way of determining the actual number of scale killed by this predator.

The cause of death of many scale could not be determined. The problems caused by this are discussed in the next section.

3.3D Seasonal variation in the causes of mortality

The seasonal variation in the major causes of mortality to the female scale are shown in the series of Figures 3.6(b) and (c), 3.7 (b) and (c), 3.8 (a), (b) and (c). The data are given in the appendix (Tables 10, 11, 12, 13 and 14 appendix).

The percentage of the total number of scale killed by coccinellids (especially *R. ventralis*, which was by far the dominant species) is shown in Figures 3.6(b) and 3.7(b). In both areas sampled and in both years R. ventralis was present from April until December, disappearing in the first season in the first week of January 1972 and in the second season in mid-December 1972. The proportion of scale killed, as shown by the number of tests bearing marks of the predator, increased from August to November. During the summer months (January - February sampling in 1972, March - April 1972 and January - March 1973) damage caused by coccinellids was uncommon. In March 1973 one population near Alverstoke Orchard was heavily attacked (45.5% of the scale were destroyed) by a species of Diomus but four other populations sampled at this time showed no damage due to coccinellids, and on these populations there were no coccinellids present. Predation by coccinellids is more fully discussed in Chapters 4 and 5.

Many scale were also killed by hymenoptera. There were at least two species (Aphycopsis spp.) which appeared to be primary parasites and these were often hyperparasitized. The complex of hymenoptera is discussed more fully in 5.6. The seasonal pattern in the percentage of female scale destroyed by hymenoptera was the reverse of that for predation by coccinellids, with peaks in the rates of parasitism occuring in summer. (Figures 3.6(c) and 3.7(c)). In some populations, more than 30% of the female scale were killed by hymenoptera in January and March (Table 11 appendix).

Larvae of S. melanochra mined a highly variable percentage of the scale, on seven occasions exceeding 40% of those examined (maximum 81.1%, tree 1842A November 1971) (Table 12 appendix). There was no seasonal pattern in the proportion of scale killed (Figure 3.8(a)).

Less than 10% of the scale were usually killed by Pseudoleucopis spp. except in January 1972 when 21.2% (range 11.7 to 28.2%) of the scale near Alverstoke were destroyed by the larvae of these flies (Figure 3.8(b)) (Table 13 appendix).

The percentages of female scale which died from unknown causes are shown in Figure 3.8(c) (Table 14 appendix).

In the population near Alverstoke the cause of death of all but about 5% of the scale was determined except in the first sampling (August 1971) and in January and March 1973 (12.5%, 32.1% and 13.3% respectively undetermined). Identification of the causes of mortality was more difficult in the populations in the Mallee Block in summer and early autumn of both years. Here the mean percentage of scale which died and for which the cause of death could not be determined was between 18.4% and 50.5%.

Female scale which had died soon after the completion of the test, before the ovaries began to expand, were frequently encountered in summer. These had a very flat appearance and none of the usual signs of parasitism or predation were present. Because of the high survival rate of the female scale when conditions were favourable, I assume these scale were either killed by the common natural enemies which did not leave their characteristic marks, by unidentified natural enemies, or by high temperatures in summer.

In January and February of both years live females were dissected from trees where many of the scale had this flat appearance and were dead. These live ones were obviously destined for the same fate as their ovaries were not developed and they contained less body fluid than normal healthy females at this stage. They were perhaps suffering from high summer temperatures as in summer the size and fecundity of the females decreased greatly (3.4).

Some females may have been killed soon after they settled either by very small larvae of some of the common predators or by spiders or mites (the latter were sometimes found under the tests of dead scale). Sometimes very small larvae of *Pseudoleucopis beneficia* or *Rhizobius ventralis* were found feeding on newly settled females as ectoparasites and when the body of the coccid had been sucked dry they left it, escaping through the caudal opening without making the usual characteristic marks on the test.

Scale were also seen where part of the top of the test had been removed, sometimes leaving only the base of the scale. In summer such damage was caused by either ants removing the body and test of the dead scale, or by the test of the scale breaking away when hymenoptera emerged from the body of the scale beneath, or by predation by the larvae of *Catoblemma*. During the first year of the survey I did not suspect that ants removed the body and test of the female scale and it was not until laboratory studies on the ants and scale revealed this behaviour that it was recognized in the field. Most scale from which hymenoptera emerged contained exit holes and only in a small number of cases was the top of the test broken off. It was not possible to distinguish between scale destroyed by ants, *Catoblemma* or the atypical damage by hymenoptera.

The larvae of the *Catoblemma* spp. were found on only two populations in February and March 1972 and were initially considered of little importance. However, in late November 1972 larvae attacked colonies of immature scale near Alverstoke Orchard and larvae of at least one succeeding generation of _Catoblemma_ persisted in the study area until March 1973. Predation by the larvae was difficult to measure and the impact of predation almost impossible to assess because of the high rate of parasitism (see above) and the reproductive malfunction of some of the female scale in late summer. No simple quantitative estimate of the percentage scale killed can be given but a full discussion of the possible predation by _Catoblemma_ is given in 5.5. In summary, larvae of _Catoblemma_ were influential in causing the extinction of the population on A6 between January and March 1973, apparently had little impact on two other populations (A10 and A12) near Alverstoke but probably killed a large proportion of the female scale in the three populations examined in the Mallee Block.

Chrysopid larvae were most active during the spring and summer (September to early January) of 1971 - 1972, when larvae were seen on the populations near Alverstoke Orchard. On one tree (Obs. 3) I estimated that 32% of the female scale of a total population of 764 in November 1971 were killed by chrysopid larvae; on the two other trees with much larger scale populations (Obs. 1: 14900, and Obs. 2: 30,200) 4% and 8% of the scale examined were destroyed by chrysopid larvae; during the second year of the survey these predatory larvae seemed to be relatively unimportant (see 5.2).

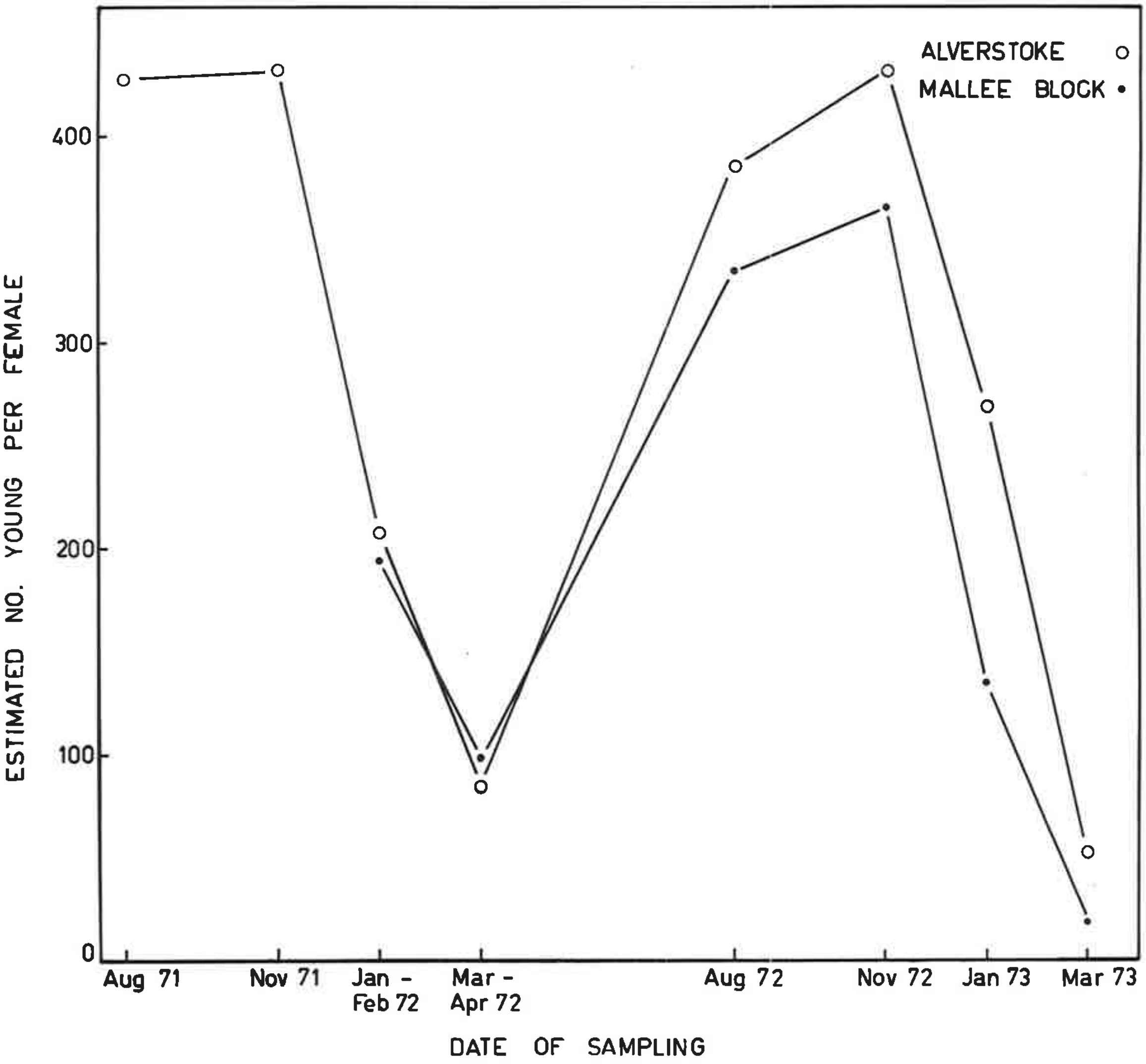
The natural enemies of _E. coriaceus_ may be divided into two groups.

Some were seasonal, being rare or absent during part of the year and yet, in some cases, appearing in large numbers and killing a large proportion of the female scale at other times. *Rhizobius ventralis*, members of the complex of hymenoptera, *Catoblemma* spp. and *Chrysopa ramburi* were such organisms. On the other hand *Pseudoleucopis beneficia* and *Stathmopoda melanochra* were present throughout the year and there was no evidence of any seasonal trends in the proportion of scale killed. Even if the absolute number of scale killed by these latter two predators is examined (giving some idea of the population of predators) there are still no seasonal trends.

Among the predators which showed seasonal patterns in activity, *R. ventralis* and the hymenoptera may be distinguished from both the *Catoblemma* spp. and *Chrysopa ramburi* by their more regular appearance and by the greater uniformity of their attack. The former were found at the same time in both years of the survey. Furthermore *R. ventralis* attacked all populations examined in August and November samplings, and in 22 of the 27 populations examined in summer the rate of parasitism by hymenoptera was over 10%. Larvae of *Catoblemma* spp. were found on only 2 of the 8 populations examined between January and April 1972 but on 10 of the 14 populations examined in the same period in 1973. Chrysopid larvae were seen on all populations of scale near Alverstoke from September 1971 to early January 1972 but were seldom seen on the populations in the Mallee Block. In the spring of 1972 they had little influence on the populations of female scale.

Figure 3.9

Seasonal variation in the fecundity (estimated from the mean length) of female *E. coriaceus* in the two study areas.


ALVERSTOKE ○
MALLEE BLOCK ●
ESTIMATED NO. YOUNG PER FEMALE
0
100
200
300
400
Aug 71
Nov 71
Jan - Feb 72
Mar - Apr 72
Aug 72
Nov 72
Jan 73
Mar 73
DATE OF SAMPLING

3.4 Seasonal variation in the fecundity of the female scale

The length of a female scale is related to the number of young she can produce (2.3A) and the mean length of the females, at the time of reproduction, varies throughout the year (2.3C). If the number of young expected is calculated from the mean size, the seasonal fluctuation in fecundity is truly remarkable. In Figure 3.9 the seasonal variation in fecundity estimated for the two areas studied is shown.

The range of fecundity for the scale near Alverstoke was from 432.7 in November 1972 to 52.5 in March 1973 (an 8 fold difference) and for those in the Mallee Block 364.7 to 18.5 (a 20 fold difference).

Although the females on the trees near Alverstoke Orchard were small in late summer, they were otherwise normal, for they produced sizeable areas of first instar nymphs. On some trees in the Mallee Block the females were extremely small and apparently suffered reproductive abnormalities for very few crawlers were produced.

In April 1972 the mean size of the female scale on 1908B was only 1.48 mm (range 1.14 to 1.88 mm). According to the equation $y = 309.16x - 494.74$, relating the length of the female scale, x, and fecundity, y, young should not be expected from females below 1.60 mm. These small females were, in fact, reproductive, for scale down to 1.14 mm not only contained several well developed embryos but sometimes dead crawlers in the ovisac. It was common to find between eight and about twenty well developed embryos in scale between 1.14 mm and 1.54 mm. Occasionally females were found which contained a large number, up to about 100, of rudimentary oocytes. These were obviously immature scale and would increase in size when development of the ovaries was completed. The population on 1908B in January 1973 and March 1973 also contained undersized females (means 1.96 mm and 1.54 mm respectively). The population on this tree was still in existence, but very small (26 females) in June 1973.

In January 1972 four live female scale were observed in the population on 1821C. These were not removed but left on the tree. They were dissected in February 1972, and were dead but with no sign of predation or parasitism. Two had dead crawlers in the ovisac. A similar procedure was followed on tree 1954B in January and February 1973 where two females (1.26 and 1.50 mm) were dissected. Once again both had died and in their ovisacs were 12 and 14 dead crawlers respectively. The quality of the crawlers produced in summer was obviously inferior as dead crawlers were not found in the ovisacs of the females at other times. On neither tree were any nymphs observed and on both trees the populations were extinguished.

The highest indices of population trend occurred when the females were most fecund. Between August and November 1971 there was, on the average, a 40 fold increase in the populations. A 12 fold increase also occurred from August to November 1972 (tree 1954B) and between November 1972 and January 1973 the population of female scale on tree A6 increased nearly 10 fold. On the other hand, the maximum changes in the number of scale between successive generations from January to March and March to August were noticeably less, the greatest index of population trend being 5.23 from January to March 1972 on 1842A. The possibility that mortality was invariably higher at the latter times can not be ruled out but the high survival rate (64.1%) of females on tree 1842A in January 1972 indicates that the lower trend indices are probably due to the lower fecundity of the scale.

3.5 Conclusions

The following conclusions may be drawn. The populations of female E. coriaceus were largest in winter and spring, and although there was a great deal of variation, there was overall a marked decrease in numbers from spring to summer in both of the study areas in both years. The females had the highest fecundity in August and November so the decrease in numbers from November to January was not caused by low fecundity.

Survival of the female scale at the time of reproduction was high at the end of winter (August) but decreased greatly in the next generation (November). The coccinellid Rhizobius ventralis destroyed over 50% of the female scale in 9 of the 13 survey populations examined in November 1971 and November 1972. An inspection of Figures 3.6, 3.7 & 3.8 indicates that this was the major predator active at this time in both years and in both study areas and was therefore not only the cause of the lower survival of the female scale in November but also the most probable cause of the decline in numbers from November to January. An examination of predation by R. ventralis on nymphs of E. coriaceus produced by females in November 1972 (4.6) strengthens this conclusion. The fact that one population which was well protected by ants, increased 10 fold from November 1972 to January 1973 is clear evidence that at this time of the year populations are capable of increasing greatly if predation by R.

ventralis is reduced. Predation by *R. ventralis* is discussed in more detail in the next chapter, where the interactions of ants and the coccinellid are examined, and also in Chapter 5 where aspects of the biology of the coccinellid are described.

Population numbers were suppressed in summer by many factors. The rate of parasitism by hymenoptera was high, and in the summer of 1972-1973 predation by *Catoblemma* was also appreciable. In summer the fecundity of the female scale was low and this was a factor of major importance in preventing the great increases in populations seen, on occasions, at other times of the year.

At any time, not only may the numbers of scale in different populations be highly variable, but so also may the population trends between successive generations. In the area near Alverstoke between November 1972 and January 1973 this variability was caused by differences in predation by *R. ventralis* which were, in turn, largely due to the variable attendance of ants. The increase in numbers on tree Obs. 1 from November 1971 to January 1972 whilst the numbers on Obs. 2 and Obs. 3 declined was probably also due to the variable attendance of ants.

CHAPTER 4

The Mutualistic Relationship between Ants and *E. coriaceus*

4.1 Introduction

The mutualistic relationship between ants and those homoptera that produce honeydew has been succinctly and comprehensively reviewed by Way (1963). He defines mutualism as an association between the ants and the homoptera they attend which is mutually beneficial without necessarily implying obligate dependence or interdependence.

Ants benefit chiefly from the large available supply of honeydew which contains not only sugars but also amino acids and amides, proteins, minerals and B vitamins. The ants may also eat the homoptera, most commonly removing dead individuals, but in some cases killing live scale or aphids.

The ants may protect the homoptera from their natural enemies or confer benefits in more subtle ways. The ants may perform important sanitary functions by removing honeydew which, if allowed to accumulate, could drown sedentary homoptera, especially when they form dense colonies. The removal of the honeydew prevents excessive growth of sooty mould which can kill homoptera or reduce the photosynthetic capability of the tree which may already be under severe stress from the enormous amounts of energy, in the form of sugars in the honeydew, that large populations of homoptera withdraw (Llewellyn, 1972). The attendance of ants has a direct stimulatory effect on the rate of feeding of homoptera and there is evidence that in at least one species it leads to increased assimilation of nutrients and increased rate of growth of the attended homoptera. The attendance of ants may also change the behaviour of the homoptera and lead indirectly to increases in the rate of growth and reproduction. Ants may also transport homoptera to uninfested trees and thus establish new colonies.

4.1A Honeydew of *E. coriaceus*

The composition of the honeydew of *E. coriaceus* has been examined by Basden (1968, 1972) who found sugars (as glucose, 33.15%), protein (2.6%), ash (containing a large array of minerals, 11.4%), esters and acids (5.0%) (47.85% not determined).

Three of the sugars had not been described before. Basden determined their structure and called these eriose (1968) and cryptose and lasiose (1972). Two others, laminaribose and turanose (Basden 1968) had not previously been recorded from natural sources. Melezitose, glucose, fructose and raffinose also occurred.

The composition of the honeydew differs from that of the sap of the tree. The sugars in the sap of several species of eucalypts consist of approximately 10% raffinose, 80% sucrose, 10% glucose and fructose (Basden 1965). The honeydew of *E. coriaceus* contains about 10% sucrose, the raffinose is unchanged (10%) and the remainder of the sugars have high molecular weights and are not found in the sap of the tree (Basden 1968, 1972).

The honeydew of *E. coriaceus* contains a wide variety of nutrients and it may be assumed from the discussion of similar honeydews (Way, 1963) that it forms a valuable food for ants.

TABLE 4.1(a) Ants collected taking honeydew or in association with *Eriococcus coriaceus*.

Species	No. of collection containing this species
Subfamily MYRMECIINAE	
Myrmecia pilosula F. Smith	1
Myrmecia pyriformis F. Smith	2
Subfamily MYRMICINAE	
Chelaner sp.	1
Subfamily FORMICINAE	
Camponotus ? consobrinus (Erichson)	8
Camponotus sp. A	2
sp. B	1
sp. C	1
Melophorus sp.	1
Notoncus hickmani Clark	1
Paratrechina minutula	1
Paratrechina sp.	1
Prolasius sp.	1
Stigmacros sp.	1
Subfamily DOLICHODERINAE	
Iridomyrmex sp.? *purpureus* F. Smith	6
Iridomyrmex glaber (Mayr)	1
Iridomyrmex sp. A	10
sp. B	16
sp. C	6
sp. D	8
sp. E	11

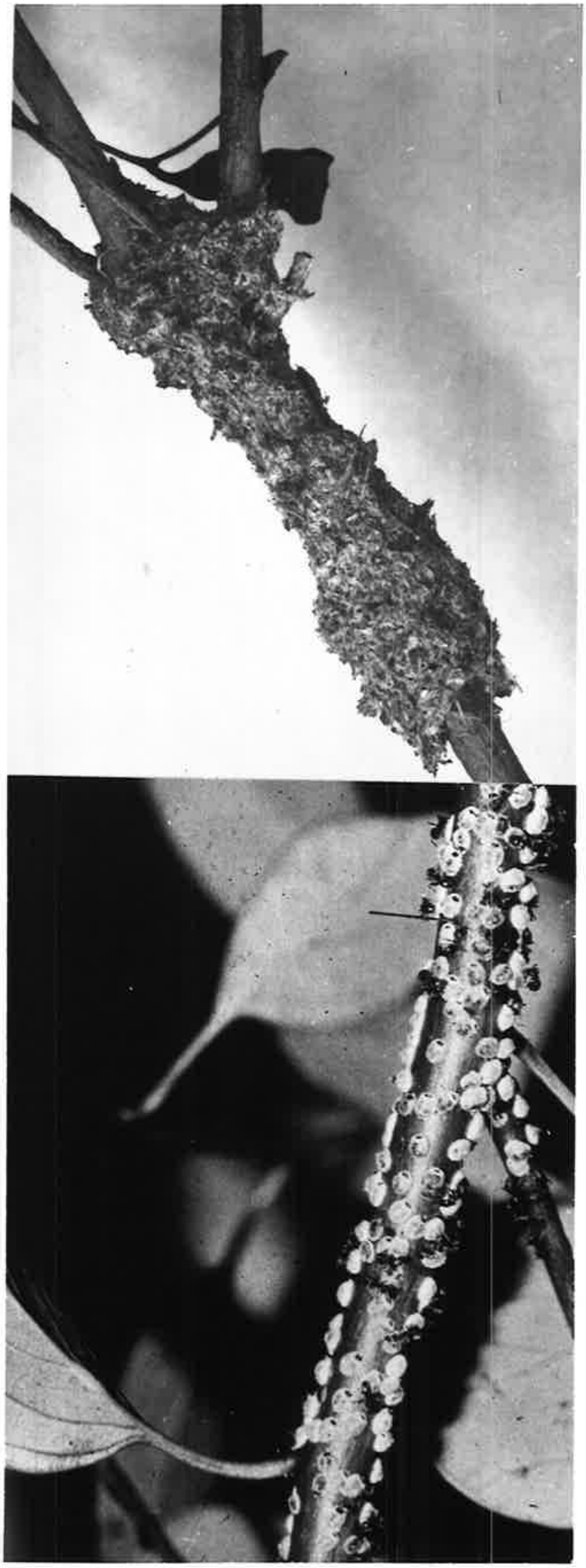
TABLE 4.1(b) Collections containing more than one species of ant.

1. *Myrmecia pilosula*, *M. pyriformis*, *Iridomyrmex* Sp. D.
2. *Myrmecia pyriformis*, *Camponotus* sp. C.
3. *Paratrechina minutula*, *Prolasius* sp.
4. *Melophorus* sp., *Iridomyrmex* sp. B.
5. *Paratrechina* sp., *Iridomyrmex* glaber.
6. *Notoncus hickmani*, *Iridomyrmex* sp. D.
7. *Camponotus* sp. A, *Iridomyrmex* sp. C.
8. *Iridomyrmex purpureus*, *Iridomyrmex glaber*.

Figure 4.1

(a) A shelter built over a small colony of E. coriaceus by Iridomyrmex glaber in Kuitpo Forest, South Australia.

(b) Iridomyrmex sp. B attending female E. coriaceus near Alverstoke Orchard. The scale have just completed the secretion of their tests.



4.1B The species of ants attending *E. coriaceus*

Collections of the ants attending *E. coriaceus* were made from the experimental areas at the Waite Agricultural Research Institute, from Kuitpo Forest, and from scale that were encountered elsewhere. In all, 72 collections of ants were made and 20 species were identified (Table 4.1(a)). Several species were sometimes collected together on the scale (Table 4.1(b)). Collections were usually made during the day but on several occasions ants were taken at night.

There were two dominant genera. *Iridomyrmex* species occurred in 58 of the 72 collections and *Camponotus* species in 12 collections. *Iridomyrmex purpureus* (Figure 1.1(c)) is easily distinguished from the other species of *Iridmoyrmex* I collected by its size. Workers of *I. purpureus* are over 8 mm long whereas workers of the other *Iridomyrmex* species I collected are below 4 mm (Figure 4.1(b)). *I. purpureus* were collected (attending *E. coriaceus*) in one area at Kuitpo Forest whereas the smaller species were found attending scale in many areas. Only three collections contained neither of these genera. Although the number of species of ants collected was fairly extensive it seems likely that more species do in fact visit *E. coriaceus*. Collections were made chiefly during the day but on those occasions when I visited scale at night other species of ants were frequently present. In November 1972 populations of scale which were attended exclusively by *Iridomyrmex* sp. B. during the day were visited by *Camponotus* sp. and *Myrmecia pyriformis* at night. The latter two species foraged if there were few *Iridomyrmex* sp. but on one tree (A6) where there were many *Iridomyrmex* sp. B at night no other species of ant was present. On several occasions in cooler weather, October, 1972, there were no *Iridomyrmex* sp. B at night on this tree and *Myrmecia pyriformis* was seen foraging at night. (It has been shown that this species of *Iridomyrmex* was more active at higher temperatures). It would seem that the presence of *Iridomyrmex* sp. B in large numbers restricted the foraging activity of these other ants. The dominance of *Iridomyrmex purpureus* over *Camponotus consobrinus* and *Camponotus* sp. was demonstrated by Calley (1969). He found that *I. purpureus* and the *Camponotus* species seldom came into contact because of differences in foraging behaviour and food preferences but whenever there was an encounter *Camponotus* fled.

If the times and circumstances of collections not containing *Iridomyrmex* spp. are examined the dominance of this group during the day in warm weather is striking. Of the three collections in which neither of the major genera were present one was made in winter (*Chelaner* sp., June 1973 when the temperature was about 14°C), and one (*Prolasius* sp. and *Paratrechina minutula*) in the late afternoon in an area dominated during the day by several species of *Iridomyrmex*. Four of the collections of *Camponotus* were made at night and four more during day in mid-winter (July 1973) on trees in the Mallee Block at the Waite Institute dominated by a small *Iridomyrmex* sp. (probably sp. B) in summer. In half of the mixed collections, 1, 4, 6 and 7, the numbers of individuals of *Iridomyrmex* greatly outnumbered those of the other species.

There was evidence even within the genus *Iridomyrmex* of shifts in the foraging activity of species. Thus *I. purpureus* was collected from one locality in Kuitpo Forest in December 1973 but on the same trees in January 1974 I. glaber was collected and no I. purpureus were seen. It was also obvious watching Iridomyrmex sp. B. near Alverstoke Orchard that shifts in the foraging behaviour occurred in hot weather. There was a definite decline in activity in the heat of the day and ants were very active at night.

Ants are a dominant faunal group in Australia (Brown and Taylor, 1970) and E. coriaceus must provide an important energy source. Ants of the genus Iridomyrmex are very common in Australia (P.J.M. Greenslade, pers. comm.) so their monopoly of E. coriaceus, at least during the day, is not surprising. Other species of ants are able to share the valuable resource by foraging in cold weather or (under some conditions) at night. Some colonies of E. coriaceus were found unattended only on some occasions in winter (June, July and August).

Some ants build shelters over the homoptera they attend (Way, 1963). I saw only one shelter (Figure 4.1(a)) which was built by I. glaber over a small colony of E. coriaceus.

In the following section the relationship between E. coriaceus and the small black ant Iridomyrmex sp. B. found most commonly in the experimental area is examined, firstly in terms of the ant/scale interaction and then in terms of the influence of ants on the predators of the scale.

It seems pertinent to mention here that in some associations it is possible that the tree also receives benefits, despite the fact that it supports a population of homoptera, for the ants attending the homoptera also remove phytophagous insects from the tree. Bradley and Hinks (1968) found that ants attending aphids on Jack Pine removed defoliators and benefited the host tree. Similarly, Room (1972), as working on mistletoe, found that workers of Crematogaster africana tending coccids, (which did not appear to reduce the vigour of the food plant) caused a substantial decrease in the damage to the leaves caused by phytophagous insects when compared with plants from which ants were excluded. The influence of ants (attending E. coriaceus) on the defoliators of the eucalypts supporting the coccids was not examined in this study. I noticed, however, that defoliation due to lepidopterous larvae on some small E. cladocalyx (carrying small populations of scale) from which ants were excluded appeared to be more severe than on trees where there were scale attended by ants. Whether the ants would have found and removed the larvae and given equal protection if there had been no scale, which is the important question, was not examined.

4.2 The influence of the attendance of ants on the rate of excretion of honeydew and the assimilation of nutrients by E. coriaceus

4.2A Introduction

Herzig (1938) found that the volume of honeydew excreted by Aphis sambuci increased three fold when the aphid was attended by Lasius niger. He also found a small increase in the rate of excretion by Aphis fabae when attended by Lasius fuliginosus. Banks and Nixon (1958) demonstrated that the rate of excretion in Aphis fabae was increased when it was tended by Lasius niger, but could find no increase in the rate of development or fecundity. They attributed the increased rate of multiplication of colonies attended by ants to indirect benefits, e.g. the ants stroked the aphids and made them less active, so that individuals which would normally disperse formed large colonies and stayed on the more nutritious growing parts of the plants. El-Ziady (1960) showed that permanently attended aphids grew faster and were more fecund than unattended aphids and she considered that ant attendance was most beneficial when the aphid was in the adult stage. However, Way (1963) considers that even in El-Ziady's experiment, aphids may have been receiving indirect benefits from the ants which, once again, pacified the aphids, allowing the formation of dense aggregations which form powerful physiological sinks, competing with the natural growing points of the plants for nutrients. These conditions are optimal for aphid growth (Way and Cammell, 1970).

Bartlett (1961) found that immature Coccus hesperidium did not benefit from attendance by Iridomyrmex humilis but he did not examine the influence of ants on the adult coccids. Way (1954) starved Oecophylla longinoda to varying degrees and then allowed them to attend colonies of Saissetia zanzibarensis. He found that the scale which developed fastest were those which were attended by ants most deprived of honeydew (and thus most attentive).

The behaviour of both E. coriaceus and the attendant ants are discussed below. The rate of excretion of honeydew and the rate of development and fecundity of tended and unattended scale were examined by simple experiments.

4.2B Behaviour of ants and E. coriaceus when excreting honeydew

The behaviour of ants (Iridomyrmex sp. B.) and of E. coriaceus was observed using first instar scale on leaf discs floating on water in plastic vials (White 1970). Each disc was seeded with 50 first-instar crawlers and observations were made after they had settled for from three to four days. As some of the crawlers left the discs and drowned the number of scale on the discs was variable. Ants were in continual attendance soon after the crawlers had settled. Ants were able to step on and off the floating discs whereas the much smaller nymphs were isolated on the discs. The discs were placed in sunlight in a glasshouse where the temperature was controlled between 18 and 24°C during the day. Observations were made on a shaded bench at 20°C. A glass slide was placed over the top of the vial, thus imprisoning the ant tending the scale. The leaf disc and ant could then be placed on the stage of a microscope and if the ant continued to tend the scale observations were made after about 3-5 minutes, when the ant had settled down.

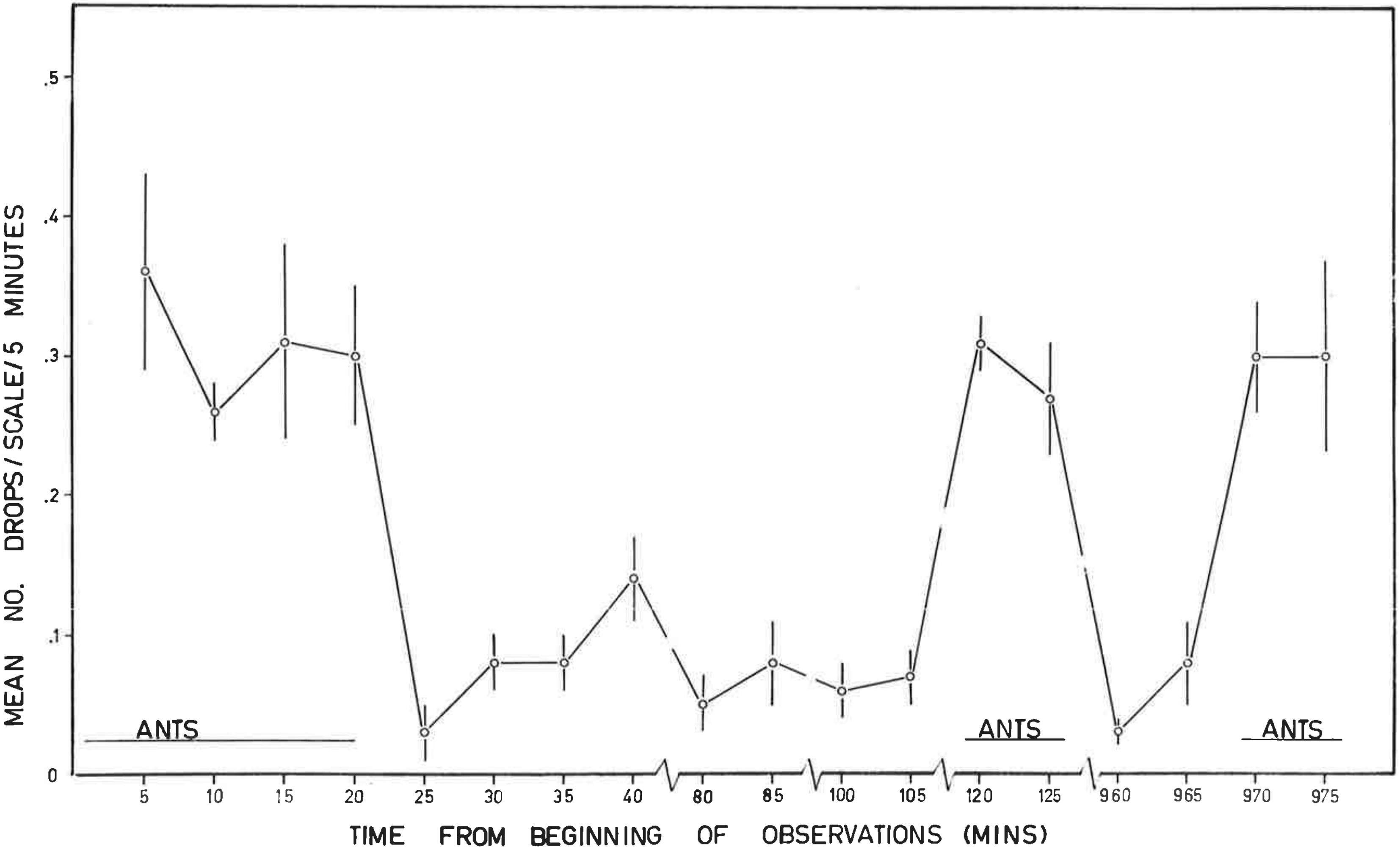
There are many similarities between the way Iridomyrmex sp. B. behaves towards E. coriaceus and the way Lasius niger tends Aphis fabae (Banks 1958). The ant moves its antennae ceaslessly; it may single out an individual nymph and stroke it but usually moves its antennae over a whole group of nymphs (the nymphs settle in dense colonies). When a nymph is about to excrete a drop of honeydew it may respond to a touch from the antennae of the ant by raising the caudal end of the abdomen. The ant normally pays special attention to such nymphs, pausing for a second or two to stroke them whereupon the nymph excretes the drop of honeydew which the ant takes up in its mandibles (sometimes using the labial palps and antennae to help the drop into its mouth). The scale respond merely to the touch of the ant for they can be made to excrete drops of honeydew by tickling them with a fine camel-hair brush. Sometimes, in its frenzied activity, the ant may cause five or six nymphs to excrete drops of honeydew and they wait with abdomens raised until the ant takes the drops. If the ant does not remove the drop of honeydew and it remains on the anus of the scale for 10-15 seconds it may be withdrawn by the scale (which is not a common occurrence), it may be lowered onto the surface of the leaf (in this case the anal setae are often used to help hold the drop), or it may be ejected a short distance by the sudden closure of the anal valves or anal ring setae. The ants not only take honeydew from the scale but also remove it from the leaf.

The anal setae of E. coriaceus are used to hold the drop of honeydew to allow the ant to take it; if the ant does not take the drop it can be forcibly ejected or lowered onto the leaf. The surface tension of the drop appears to be considerable and in many cases the drop is ejected by the sudden closure of the ring setae rather than the anal valves. It is difficult to see how the scale could hold the excreted drop and then eject it without the setae. The value of holding drops is obvious, in that the ant and scale are brought into the closest possible contact and thus the ant can give maximum protection to the scale. By ejecting the drops which are not removed by the ants, the scale avoids self-contamination with the honeydew.

The ants take about 10 minutes to feed to repletion when provided with unlimited honeydew. As an ant feeds its abdomen becomes more and more distended and the plates of the gaster are eventually separated by areas of clear transparent intersegmental membrane. This condition is markedly different from the normal black and compact gaster. All of the foraging workers seem able to assume the replete condition, common

Figure 4.2

The rate of excretion of honeydew by nymphs of *E. coriaceus* when attended by ants and when ants are absent. Standard errors are marked.


MEAN NO. DROPS / SCALE / 5 MINUTES
.5
.4
.3
.2
.1
0
ANTS
ANTS
ANTS
5
10
15
20
25
30
35
40
80
85
100
105
120
125
960
965
970
975
TIME FROM BEGINNING OF OBSERVATIONS (MINS)

behaviour in the Dolichodorinae (Wheeler, 1910).

The behaviour of the ant changes after feeding. Before feeding it wanders somewhat erratically to a suitable patch of scale, but after feeding it is remarkably "single minded" and walks straight down the stem.

4.2C The influence of ant attendance on the rate of excretion of honeydew

When the ant was tending the first instar scale on the leaf disc a count of the number of drops excreted by all the scale over a five minute interval was made. This was repeated on four consecutive occasions and then the ant was removed from the leaf disc. Four more similar counts were made without the ant. The disc was set aside for 80 minutes after which two counts were made and two more after 100 minutes, then an ant was allowed to tend the scale again and two more counts were made. Ants were excluded for 16-18 hours and the excretory rate re-examined. Finally ants were allowed to tend the scale again. As the discs had differing numbers of scale (some crawlers walked off the discs and drowned) the rate of excretion of honeydew is expressed in drops/scale/5 minutes. Rates of excretion were measured on nymphs on five discs.

The rates of excretion during the course of the experiment are shown in Figure 4.2. For each of the five discs the pattern of excretion was the same with ants stimulating the scale to produce five to six times the number of drops they did when unattended. The inhibition of excretion when ants were absent was not temporary and persisted for at least 18 hours.

In each trial the rate of excretion rose almost immediately after the ants began attending the scale.

There appear to be two sorts of excretory behaviour by the scale. One is that already mentioned, when the drop is slowly produced and either held, then placed on the leaf or flicked a short distance. This occurs when ants are present. When there are no ants the drop is forcibly and instantly ejected a considerable distance (6-10 mm). Both patterns occur in tended and unattended scale colonies but to different extents. The table below shows the change in excretory patterns.

Changes in pattern of drop excretion when ants are present and when they are absent.

(n = total number of drops excreted)

Ants Present	% Drops excreted and at least temporarily held	% Drops Ejected
n = 379	98.2	1.8
Ants Absent		
n = 120	20.0	80.0

The drops produced when the ants were absent were not larger than those excreted when the ants were in attendance and both were about .013 mm in diameter (although exact measurement was difficult). The amount of honeydew excreted when ants were present was thus approximately five times the amount excreted when the scale were unattended.

4.2D The influence of ant attendance on rate of growth and fecundity of E. coriaceus

The influence of ants on the rate of development and reproduction of E. coriaceus was examined in the glasshouse under conditions similar to those used for the observation of scale on leaf discs.

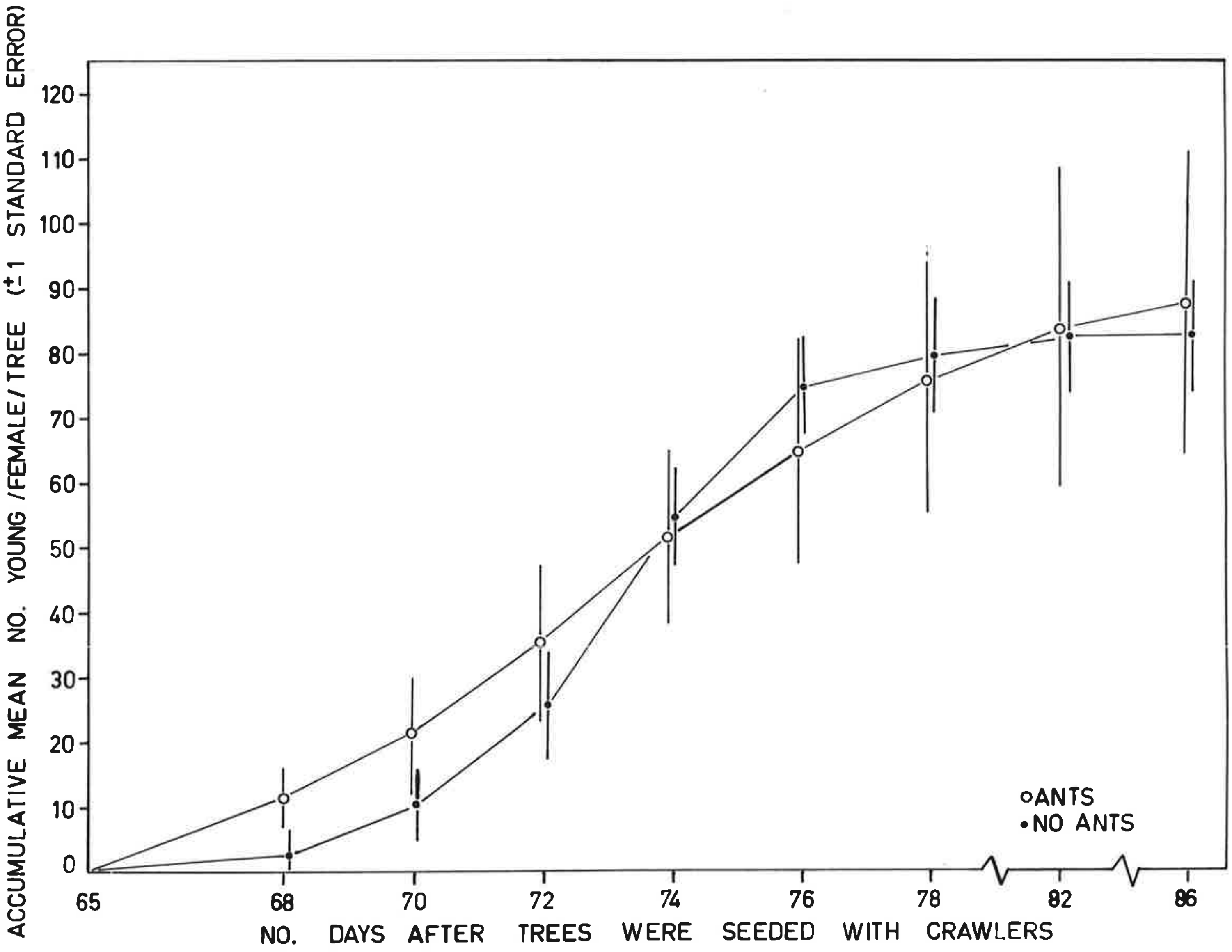
Care was taken to ensure that the scale received no benefits from the ants apart from direct stimulation of the feeding rate (as shown by the increase in the rate of excretion of honeydew). The ants were allowed to attend the scale throughout their life from the time the first instar crawlers settled until they, as females, completed reproduction. The densities of the scale on the trees were so low that even on the unattended trees there was no significant accumulation of honeydew until reproduction by the females was almost completed and large colonies of nymphs had settled. Thus the scale on the attended trees received no indirect benefits from the removal of honeydew. When the female scale settled there was no difference in the configuration or density of the colonies with and without ants and no difference in the parts of the trees occupied by the scale. Any indirect effects of the ants, such as may have occurred in El-Ziady's (1960) experiments were thus avoided.

Ten small potted E. cladocalyx were divided into two similar groups. The trees to have ants excluded were stood on inverted pots in basins of water. Ants were attracted to the other trees by placing small drops of honey on the stems. When ants were visiting the trees regularly both groups were seeded with 50 first-instar scale per tree. Ants attended the scale throughout the experimental period. Care was taken to avoid

Figure 4.3

Cumulative mean number of young produced/female *E. coriaceus*/tree when the scale were attended by ants and when they were unattended.

Standard errors are marked.


ACCUMULATIVE MEAN NO. YOUNG /FEMALE / TREE (±1 STANDARD ERROR)
0
10
20
30
40
50
60
70
80
90
100
110
120
65
68
70
72
74
76
78
82
86
NO. DAYS AFTER TREES WERE SEEDED WITH CRAWLERS
○ANTS
•NO ANTS

any possible temperature gradient in the glasshouse and the position of the pots was altered during the experiment to ensure that all scale enjoyed, as nearly as possible, the same conditions.

The scale in both groups began reproducing 65 to 66 days after the start of the experiment. At this time there was no significant difference in the number of females surviving on the two groups of trees, those trees without ants having a total of 49 living females and those with ants a total of 48.

The numbers of crawlers on the trees were counted every other day. The cumulative mean number of young per female per tree produced in each group of trees over the period of reproduction is shown in Figure 4.3. There was clearly no difference in the total mean number of young produced between the ant-attended and unattended females. There was also no difference in the rates of reproduction, for the difference between the mean number of young/female/tree 68 days after the beginning of the experiment on ant-attended (11.45 young/female/tree) and ant-free trees (2.61 young/female/tree) was not significant ($t = 1.83$; 8d.f.; N.S.). The numbers of young produced per female per tree were highly variable in both treatments.

As the nymphs developed on the trees where there were no ants there was a heavy accumulation of honeydew. Observations revealed that even under extreme conditions only 6.5% of the total larvae produced on the unattended trees were trapped by the honeydew. Significant numbers of crawlers were never trapped in natural populations in the field. When there were few ants to remove the honeydew, as sometimes occurred in late winter, it was removed either by showers of rain or by flies, especially Calliphora spp. which were seen in large numbers (up to 50 flies per tree on occasions). Hymenoptera may also feed on the honeydew. Newstead (1903) made similar observations in England. On some trees sooty mould did accumulate but this did not appear to affect either the scale or the tree.

The attendance of the ants most commonly found in the experimental area (Iridomyrmex sp. B) did not increase the fecundity of the female scale. There was also no definite increase in the rate of development of the attended scale. Furthermore the removal of honeydew and other sanitary functions performed by the ants seemed of little importance. These ants do not transport the scale and did not build shelters for them. If these ants were to have any influence on the survival of E. coriaceus it would have to be mainly through protection afforded to the coccid from its natural enemies.

4.3 The influence of ant-attendance on the survival of E. coriaceus in the field

Way (1963) suggests that when homoptera are scarce ants attend them more assiduously; homoptera in small populations are therefore better protected from their natural enemies than homoptera in large populations. If this is the case, then one would expect to find that:

1. The attendance of ants increases the survival of E. coriaceus in the field.
2. The ant/scale ratio decreases as the population of E. coriaceus increases.

3. Survival in small attended populations of _E. coriaceus_ is higher than that in large attended populations.

I decided to test the first hypothesis by excluding ants from some scale populations. I tested the second and third hypotheses by varying the population sizes of homoptera.

Trees in the plantation of 50 eucalypts near Alverstoke Orchard were used (see 1.3) and at the time of the experiment they were 2 m high. At one end was the plot of 10 _E. cladocalyx_ containing trees used for the long term population study and at the beginning of the experiment several of these had large scale populations. These populations were destroyed and used to seed the experimental trees.

Trees were seeded with two sizes of populations, the larger containing two to four times the number of scale than the smaller. A complete randomized block design was used with one tree in each block randomly assigned to one of the four treatments, which were:

1. Ants present: high scale population
2. Ants present: low scale population
3. Ants absent: high scale population
4. Ants absent: low scale population

This design was used to eliminate any gradient effect caused by the possible high population of predators, parasites or ants on the old-established populations at one end of the rows.

Trees were seeded with _E. coriaceus_ (second instar nymphs) in early September. Twigs bearing the larvae were tied in the branches of the experimental trees and as the twigs dried out the larvae left them and established new populations. Initially 10 trees were seeded for each treatment. This was necessary because of the varied success in establishing populations of suitable sizes. Five blocks (of four trees each) were eventually chosen for the experiment on the basis of having approximately similar numbers of scale in the two population-categories. Some observations were also made on the other trees.

The trees to have unattended scale populations were pruned so that their foliage did not touch the ground or neighbouring trees (thus forming a bridge for ants). The stems were banded with tanglefoot, and later grease, which had to be applied regularly throughout the experiment. Throughout the experiment the trees had to be pruned regularly and the grass removed from beneath so that tall grass stems did not touch the trees. On several occasions these precautions failed but the ants were quickly removed.

As the extent and causes of mortality can be most easily estimated by examining the female scale, ants were allowed to attend all populations until the females had settled in some numbers and begun secreting their tests. Ants were then excluded from the chosen trees.

The numbers of scale were estimated as described in 3.1. The stratified method of sampling was not used.

The numbers of survivors were estimated using two methods. Where possible, i.e. in small colonies or on those trees with small populations, direct counts of the survivors were made. On each of the trees which were seeded with large populations samples each containing about 50 scale were removed at random from four of the larger colonies. The survival rate in each of these colonies was determined from the sample taken from it and the number of survivors in each colony estimated. If there were more than four large colonies the number of females surviving in the other colonies was estimated by multiplying the number of scale in these colonies by the mean survival rate calculated from the four samples. The numbers of survivors shown in Table 4.2 were thus arrived at by both census and sampling and represent the best possible estimate I could achieve. Many of the female scale which were reproducing had first instar coccinellid larvae in their ovisacs. These were consuming the crawlers as they were produced, and as far as their contribution to the next generation was concerned, such females might have been regarded as dead. For the sake of simplicity, however, only the survival of the females was considered.

I was also interested in the causes of mortality and these were ascertained by direct observation of the scale on the trees (for some of the very small populations) and by the examination of the samples removed from the large colonies to estimate survival. A preliminary examination (in the field) of colonies on the trees with large populations, both attended and unattended by ants, had indicated that the causes of mortality in small colonies were possible different from those in large colonies. Thus four small colonies (chosen at random) were also removed from the trees with large scale populations. The smaller colonies which were sampled contained from 8 to 31 scale (mean 17.7), most having between 10 and 20 scale. The larger colonies sampled had in excess of 50 scale. Four colonies on most of those trees with small populations were also chosen at random and examined. Samples were kept in a refrigerator

TABLE 4.2 Overall results. The influence of *Iridomyrmex* sp. B on the survival of female *E. coriaceus*.

Ants present. Small scale population				Ants absent. Small scale population			
Tree No.	Initial no. female scale	No. female scale surviving	% survival	Tree No.	Initial no. female scale	No. female scale surviving	% survival
A1	362	3	.8	NA1	208	0	0
A2	217	20	9.2	NA2	195	0	0
A3	264	3	1.1	NA3	311	0	0
A4	96	3	3.1	NA4	176	0	0
A5	82	1	1.2	NA5	20	4	20.0
			3.1				4.0
Ants present. Large scale population				Ants absent. Large scale population			
A6	1147	426	37.1	NA6	714	0	0
A7	914	291	31.8	NA7	1030	67	6.5
A8	705	212	28.3	NA8	563	53	9.4
A9	614	127	20.7	NA9	663	32	4.8
A10	1348	663	49.2	NA10	2844	1512	53.2
			33.4				14.8

TABLE 4.3 The influence of ant attendance (and colony size) on
(a) survival of female *E. coriaceus*.

ANTS			NO ANTS		
Tree	% survival in large colonies	% survival in large colonies	Tree	% survival in large colonies	% survival in large colonies
A6	29.0	10.9	NA6	0	0
A7	26.3	14.9	NA7	7.3	0
A8	30.6	17.1	NA8	8.2	4.2
A9	10.4	17.9	NA9	4.5	2 2
A10	57.1	7.4	NA10	73.2	8.2
Mean	30.68	13.64	Mean	18.64	2.92

(b) Predation by coccinellids.

ANTS			NO ANTS		
Tree	% scale killed in large colonies	% scale killed in small colonies	Tree	% scale killed in large colonies	% scale killed in small colonies
A6	39.7	73.4	NA6	100.0	100.0
A7	47.0	83.0	NA7	59.8	98.8
A8	41.0	68.3	NA8	57.2	84.5
A9	60.4	74.6	NA9	62.1	79.1
A10	18.3	83.3	NA10	19.1	90.6
Mean	41.3	76.5	Mean	59.6	90.6

(c) Parasitism by *Pseudoleucopis beneficia*.

ANTS			NO ANTS		
Tree	% scale killed in large colonies	% scale killed in small colonies	Tree	% scale killed in large colonies	% scale killed in small colonies
A6	14.9	10.9	NA6	0	0
A7	5.2	2.1	NA7	5.3	0
A8	9.7	2.4	NA8	6.9	0
A9	20.7	0	NA9	4.0	1.1
A10	5.7	9.3	NA10	1.0	0
Mean	11.24	4.94	Mean	3.44	.22

TABLE 4.3(d) The influence of ant attendance (and colony size) on number of scale mined by *Stathmopoda melanochra*.

ANTS			NO ANTS		
Tree	% scale mined in large colonies	% scale mined in small colonies	Tree	% scale mined in large colonies	% scale mined in small colonies
A6	13.7	0	NA6	0	0
A7	12.5	0	NA7	16.6	0
A8	2.8	0	NA8	3.1	0
A9	0	0	NA9	3.4	0
A10	17.1	0	NA10	1.5	0
Mean	9.22	0	Mean	4.92	0

(e) Parasitism by hymenoptera.

ANTS			NO ANTS		
Tree	% scale killed in large colonies	% scale killed in small colonies	Tree	% scale killed in large colonies	% scale killed in small colonies
A6	.4	3.1	NA6	0	0
A7	2.6	0	NA7	6.5	1.2
A8	2.8	0	NA8	5.0	0
A9	5.5	3.0	NA9	4.5	3.6
A10	1.7	5.6	NA10	2.6	1.2
Mean	2.60	2.34	Mean	3.72	1.2

(f) Scale killed by unidentified causes.

ANTS			NO ANTS		
Tree	% scale killed in large colonies	% scale killed in small colonies	Tree	% scale killed in large colonies	% scale killed in small colonies
A6	.7	1.6	NA6	0	0
A7	6.5	0	NA7	4.5	0
A8	13.2	12.2	NA8	11.9	22.5
A9	3.0	4.5	NA9	6.2	13.2
A10	0	0	NA10	2.6	0
Mean	4.68	3.66	Mean	5.04	7.14

until they could be examined. Estimates of mortality and survival were made by using the total number of scale sampled from the four colonies in each stratum.

There are thus two estimates of survival for the large populations, those presented in Table 4.2 and those presented in Table 4.3(a); the former are estimates for the whole population and the latter direct measurements for colonies on trees with large populations. The results from both methods are discussed.

The populations were sampled on 17th and 18th of November when areas of nymphs appeared on many of the trees with high scale populations. Further observations were made on the fate of the females and the young they produced. Trees on which the population was apparently extinguished were visited throughout December to see if there were, in fact, any survivors.

4.3A Results

The total number of scale on each tree, the number of survivors and percentage survival are given in Table 4.2. Bartlett's test on the percentage surviving indicated that the variances were not homogeneous ($\chi^2 = 8.844$; 3 d.f.; $p < .05$). No attempt was made to transform the data because of Li's (1964) comments. He considers both the angular transformation (page 511) and the square root transformation (page 515) of little value.

Because the design was a complete randomized block I was able to pair values. Thus percentage survival in each of 10 ant-attended populations was paired with percentage survival in the appropriate unattended population (the influence of population size being neglected) e.g. A1 - NA1, A2 - NA2 etc. The attendance of ants caused a significant increase in the survival of the female scale. Mean percentage survival for the 10 ant-attended populations was 18.3% and for the 10 unattended 9.4% ($t = 2.514$; 9 d.f.; $p < .05$).

The first question can therefore be easily answered as ant-attended populations had a higher survival rate than unattended populations. To see why this was so the causes of mortality in the ant-attended and unattended populations were compared.

4.3B The influence of ant attendance on survival and extent and causes of mortality

The data from the samples removed from large and small colonies on the trees with large populations (Table 4.3) are now discussed. The influence of ants is examined by using paired observations (and the t test): between percentage survival in large colonies on the ant-attended and ant-free tree in the same block and similarly for small colonies.

a. Survival

Survival in colonies attended by ants was higher than in unattended colonies (mean percentage survival 22.2% and 10.8% respectively, $t = 3.02$; 9 d.f.; $p < .01$).

b. Mortality caused by the natural enemies, especially coccinellids

More scale were killed by coccinellids in colonies not attended by ants than in ant-attended colonies (75.1% as opposed to 58.9%, $t = 2.720$;

9 d.f.; $p < .025$).

Pseudoleucopis beneficia destroyed 8.1% of scale attended by ants compared with 1.8% of those unattended ($t = 3.29$; 9 d.f.; $p < .005$).

There was no difference in the percentage of scale killed by S. melanochra in ant-attended or ant-free colonies (Table 4.3(d)); neither was there any difference in the rate of parasitism of scale by hymenoptera (Table 4.3(e)), or in the percentage of scale which died of indeterminable causes (Table 4.3(f)).

c. Summary

The survival rate of the female scale at the time of reproduction was significantly higher in colonies attended by ants than in those not attended by ants. This is in agreement with the census of total populations and survivors previously described. The presence of ants caused a significant and substantial reduction (16.2%) in the percentage of scale killed by coccinellids (chiefly R. ventralis). Conversely there was a higher proportion of scale killed by P. beneficia on ant-attended colonies. The difference (6.3%) is not sufficient to reduce the value of the protection the ants give the scale. Ant attendance had no influence on the proportion of scale killed by S. melanochra, hymenoptera or those that died from indeterminable causes.

The interaction between the ants attending the scale and R. ventralis is discussed in detail elsewhere. The increase in parasitism by P. beneficia when ants were present was probably due to the fact that under these conditions the coccinellids were less effective and the fly parasite had greater opportunity to complete development. It is impossible to

TABLE 4.4 Ant attendance. Comparison of stem traffic and the numbers of ants actually attending *E. coriaceus*.

No. ants attending *E. coriaceus*	Rank	Stem Traffic	Rank
1	1.5	6	1
1	1.5	16	6
2	3	13	4
3	4	15	5
6	5	44	8.5
12	6	44	8.5
16	7	11	3
20	8	10	2
37	9	42	7
85	10	104	10

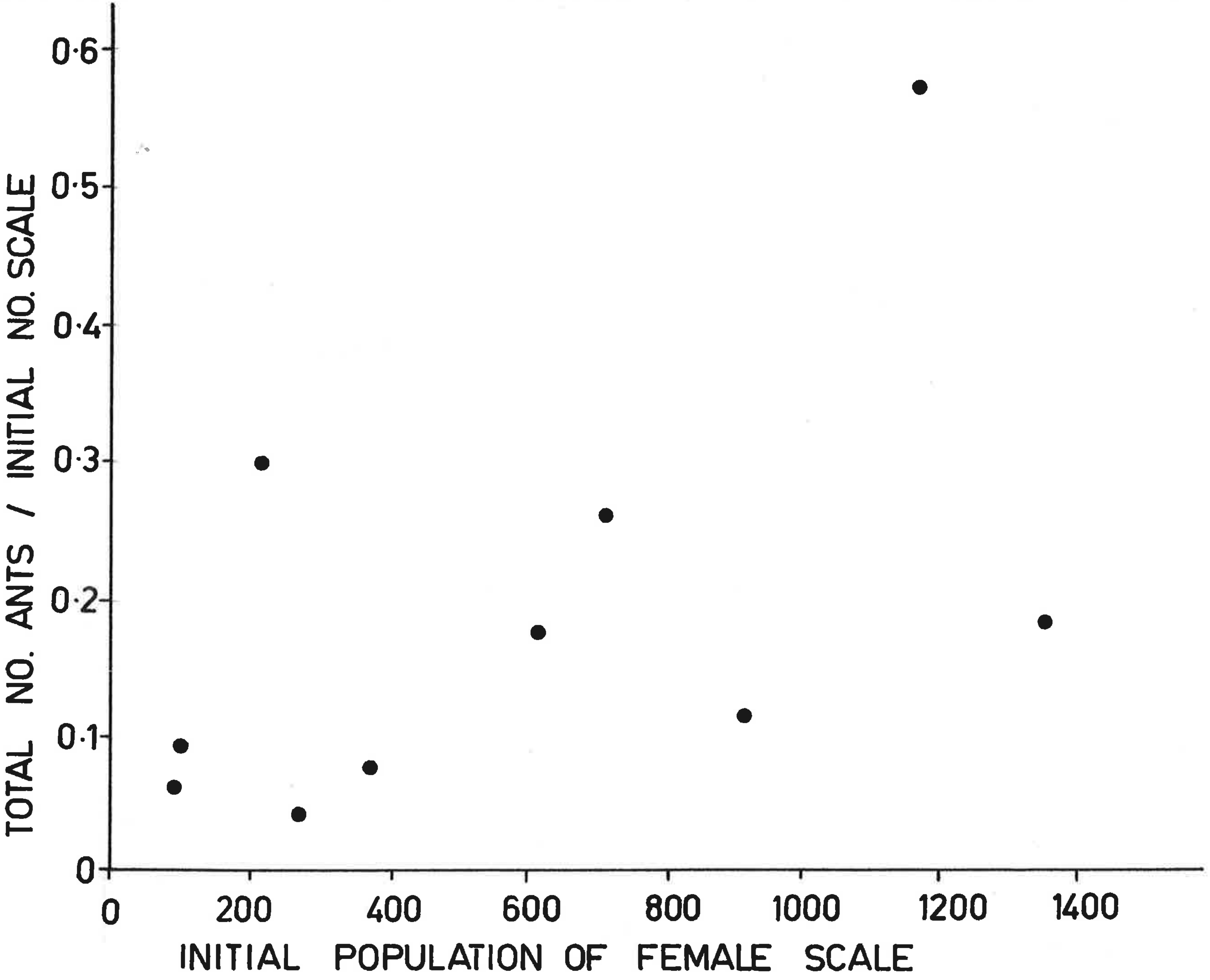
rs, Spearman rank correlation coefficient = 0.412 (N.S.)

TABLE 4.5 The relationship between initial numbers of *E. coriaceus* and total numbers (six counts) of ants in attendance.

Tree	Number of scale	Number of ants
A5	82	5
A4	96	7
A2	217	65
A3	264	12
A1	362	28
A9	614	106
A8	705	184
A7	914	114
A6	1147	655
A10	1348	244

Figure 4.4

Ant/scale ratios plotted against the number of female scale to show that there is no decreasing trend as the size of the homopteran population increases.



TOTAL NO. ANTS / INITIAL NO. SCALE
0·6
0·5
0·4
0·3
0·2
0·1
0
0
200
400
600
800
1000
1200
1400
INITIAL POPULATION OF FEMALE SCALE

make any absolute statements about the influence of ants on rates of parasitism because of the dominance of R. ventralis and the inevitable competition for prey e.g. if there had been no coccinellids present hymenoptera may well have destroyed many more scale in colonies not attended than in those attended by ants.

4.4 The numbers of attending ants

4.4A Ant attendance in the major experiment

The second question can now be asked i.e. does the ant/scale ratio decrease as the population of E. coriaceus increase?

At intervals of approximately a week the number of ants attending the scale was counted. Until the 11th October counts were made of the ants crossing a line on the base of the tree. Counts were made at 10.45 a.m., a time when large numbers of ants are active at this time of the year (see 4.5B), and consisted of four one minute observations on the traffic moving in either direction over the line. This method of measuring ant activity has been widely used (e.g. Steyn, 1956).

On 11th October, counts were made of the ants actually tending the scale in the crowns of the trees immediately after the traffic count had been completed. Table 4.4 shows the results and the relative rankings for stem and crown counts. There was no correlation between the ranks of the numbers moving on the stem and the ranks of those tending the scale (Spearman Rank Correlation. Siegel, 1956).

Although the variation in the number of ants moving on the stems of five of the trees was only between 10 and 16 ants per 4 minute period,

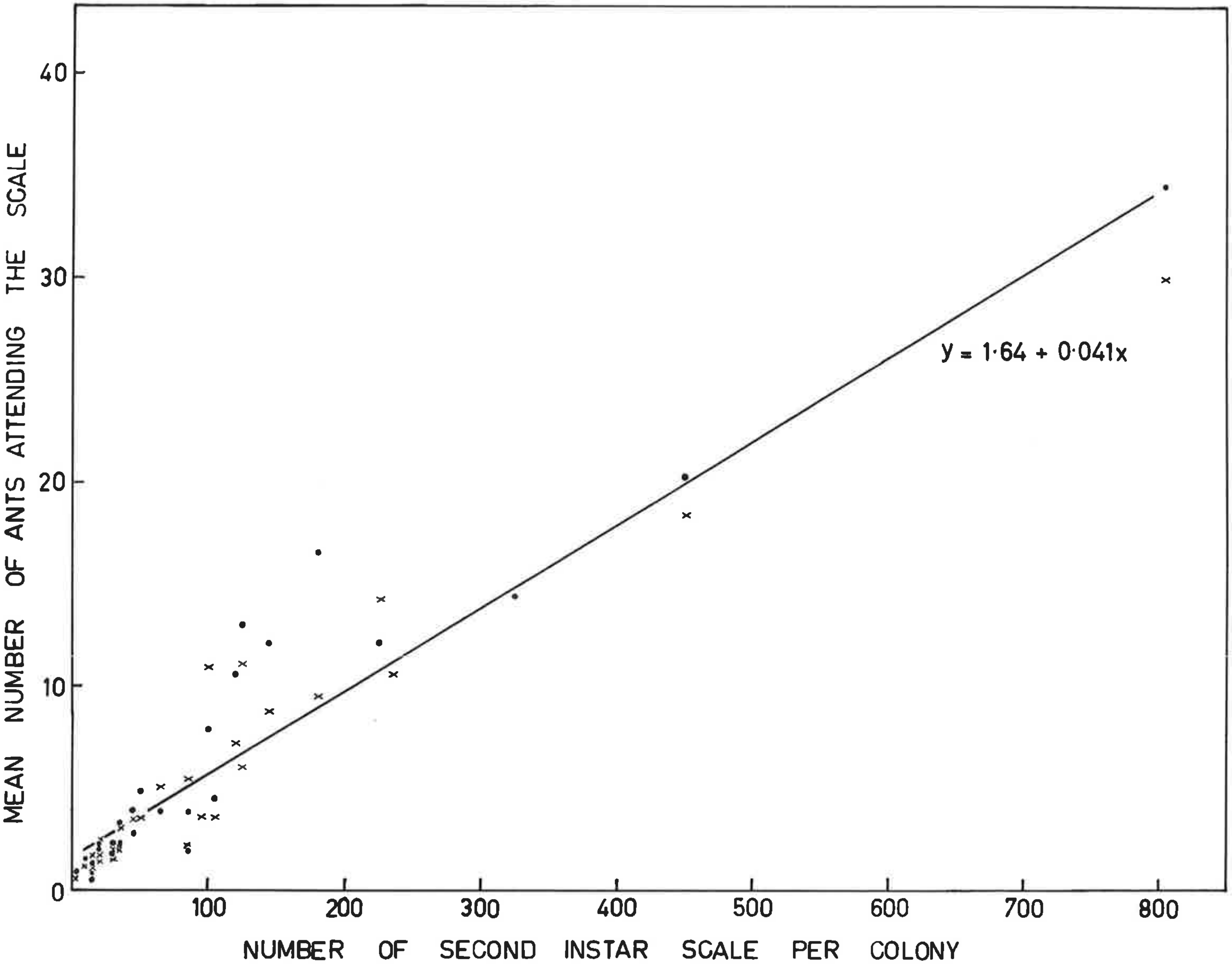
Figure 4.5

The influence of the number of second instar nymphs of *E. coriaceus* in a colony on the number of ants attending them.

Note: X data for 15th March 1973

● data for 16th March 1973

(Note: If the ant scale ratio, R, is calculated from the regression $y = a + bx$ where y = number of attendant ants and x = number of scale the plot of R against x is a hyperbola).


MEAN NUMBER OF ANTS ATTENDING THE SCALE
NUMBER OF SECOND INSTAR SCALE PER COLONY
y = 1·64 + 0·041x
0
10
20
30
40
100
200
300
400
500
600
700
800

the conclusion that there was a significant difference in the rankings of stem and crown counts seems realistic, for two trees which had a large number of ants (44/4 minute period) moving up and down the stems had few ants tending the scale (see Table 4.4). This was because the ants were also tending psyllids and leafhoppers (family Eurymelidae) on these trees.

From 11th October until 18th November six counts of the ants actually tending the scale were made. The ant/scale ratio was determined by dividing the total number of ants seen on each population in the six counts by the initial number of female scale in the population. The results are shown graphically in Figure 4.4. There is no evidence that the ant/scale ratio decreases as the initial number of scale increases; there is no significant relationship between the two variables.

4.4B The relationship between numbers of scale and numbers of ants more clearly defined

It seems worthwhile to examine more closely the influence of the numbers of scale on the numbers of ants attending them. Flanders (1951) seems to be the only person to comment on this relationship. There is a correlation ($r = 0.745$; 8 d.f.; $p < .05$) between the number of ants in attendance on a population of scale and the initial number of female scale (Table 4.5). The results are not precise because scale died or were killed during the observations and the number of living females would have been different from the initial number of females. The relationship between the number of scale and the number of ants attending them was therefore studied using early second instar nymphs of E. coriaceus where the number of living individuals could be determined in the field using a hand lens.

In March 1973 six populations of scale were establishing on trees in Alverstoke Orchard. The scale were second-instar nymphs and were seeded in the usual manner. By March 15th suitable populations were established and the number of scale in each colony was counted. Five counts were made of the ants tending each colony between 10.30 a.m. and 11.00 a.m. for two consecutive days. The trends in the mean number of ants attending both individual colonies and populations on trees for both days were similar and the data were pooled. The regression of the number of ants in attendance on the number of scale is highly significant for individual colonies ($F_{1, 58} = 54.04$; $p < .005$; Figure 4.5) and also, of course, for tree populations.

Thus ants responded to the quantity of food (i.e. honeydew) available so that, in the experimental area, generally the more scale that were present the greater the number of ants attending them.

4.4C Comparison of survival in small and large attended populations

If the ant/scale ratio does not decrease as the number of scale increases then survival in small populations of E. coriaceus ought not to be greater than survival in large populations. Survival in small populations was in fact much less (mean 3.13%) than survival in large populations (mean 33.4%). Ants protected the scale in large populations from predation by coccinellids (Table 4.3(b)) but they did not protect the scale in small populations from coccinellids (see below). There is no significant difference between percentage of scale killed by coccinellids in small attended and unattended populations.

Percentage of female *E. coriaceus* killed by coccinellids in small populations

Ants present		Ants absent	
Tree	% female scale killed	Tree	% female scale killed
A1	72.2	NA1	73.4
A2	87.2	NA2	56.6
A3	91.7	NA3	100.0
A4	97.5	NA4	83.1
A5	90.5	NA5	80.0
Mean	87.8	Mean	73.6

The following summary may be made. The attendance of ants increased the chances of survival of scale in small and in large populations. Although only 3.1% of female scale in small attended populations survived, each of the five populations contained survivors whereas only one of the small unattended populations contained survivors.

There was no evidence that scale in small populations were better attended by ants or better protected than scale in larger populations. The opposite was true, large populations of homoptera attracted large numbers of ants. Percentage survival in these large populations was higher than in the smaller populations. Further comments are made in the discussion at the end of this chapter.

It is obvious that the protection afforded by ants was far from perfect. An enquiry into the life history and behaviour of the coccinellid *Rhizobius ventralis* showed why this was so. There were several species of coccinellids in the experimental plots but *R. ventralis* was by far the most abundant (see 5.3).

4.5 The interactions between ants and predators, especially *R. ventralis*

4.5A Resume of life history of *Rhizobius ventralis*

The egg is nearly always laid beneath the test of the living female scale. The first instar larvae may feed on the body of the female scale, but most commonly feed on the first instar nymphal scale as they are produced in the ovisac. The coccinellid larvae may moult once or twice under the female scale where the egg was laid, before emerging to the outside world. They may also leave one female and enter the test of others by crawling through the caudal opening. The first two instars are often spent entirely concealed beneath the test of the scale and the larger larvae are cryptic, hiding in dead scale or under loose bark. They pupate under loose bark on the stem of the tree. Thus all the immature stages spend much of their time concealed. The life history is described in more detail later, in 5.3.

4.5B The diurnal rhythms of activity in *Rhizobius ventralis* and and *Iridomyrmex* sp. B.

As the adults and larvae of *R. ventralis* were rarely seen on ant attended trees during the day and yet killed a considerable number of scale, I concluded that they must emerge and feed at night when it was

Figure 4.6

Mean number of ants (attending scale) per tree (November 1972), showing a typical bimodal pattern of activity during the day.

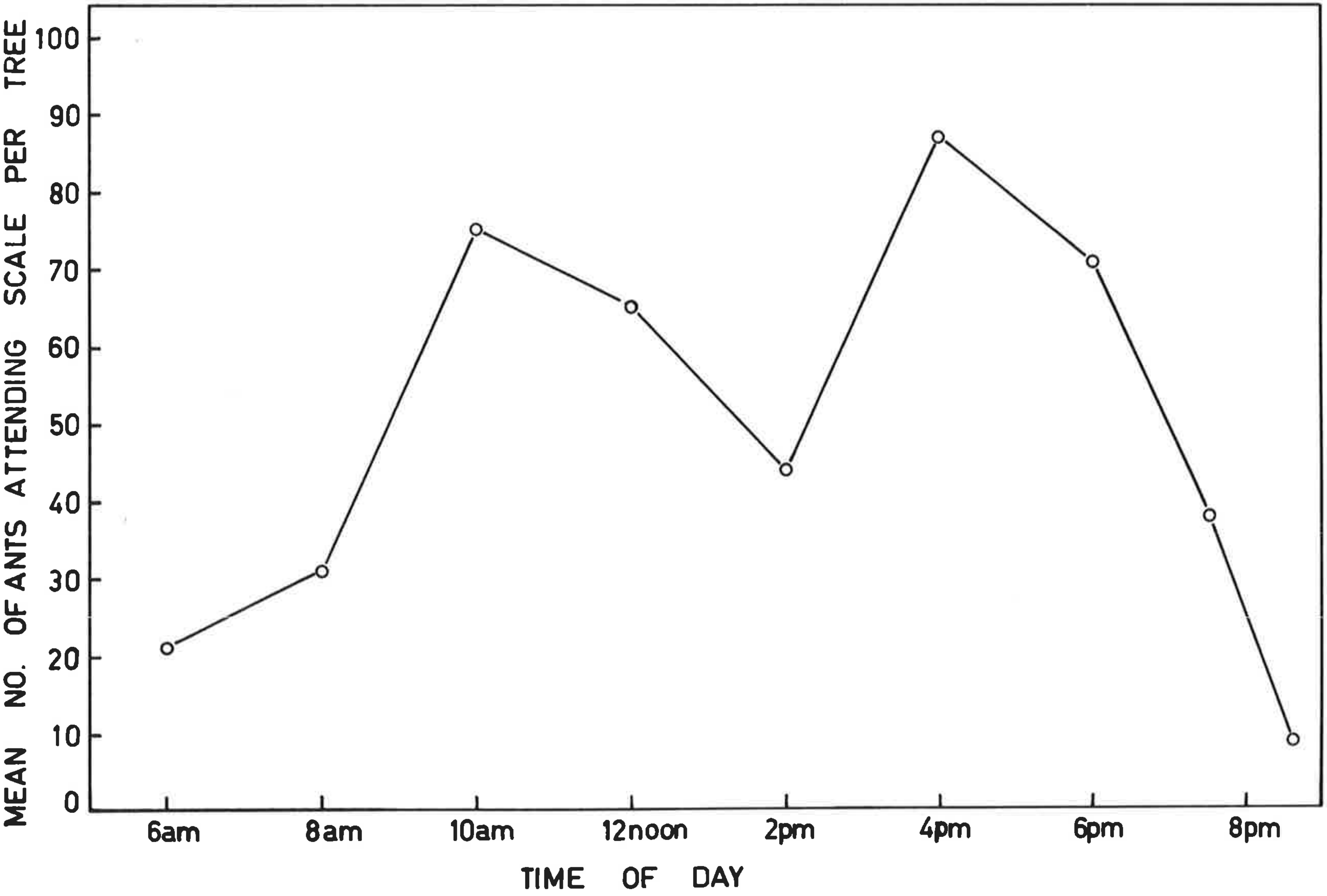

MEAN NO. OF ANTS ATTENDING SCALE PER TREE
0
10
20
30
40
50
60
70
80
90
100
6am
8am
10am
12noon
2pm
4pm
6pm
8pm
TIME OF DAY

TABLE 4.6(a) Numbers of *R. ventralis* larvae and adults at different times of the day on attended and unattended populations. Totals for 8 trees (7 November 1972).

Time	6a.m.	8a.m.	10a.m.	12noon	2p.m.	4p.m.	6p.m.	7.30p.m.	8p.m.	8.30p.m.
ANTS										
adults	1	0	0	0	0	0	1	1	4	7
larvae	0	0	0	0	0	0	0	3	4	3
NO ANTS										
adults	0	0	1	3	0	0	1	4	6	3
larvae	3	1	1	3	2	4	2	3	4	5

TABLE 4.6(b) As above for 27th and 28th November.

Time	27th 10a.m.	27th 6.30p.m.	27th 9p.m.	28th 10a.m.	28th 9p.m.
ANTS					
adults	2	1	1	0	1
larvae	1	5	16	1	14
NO ANTS					
adults	0	0	0	1	0
larvae	17	25	16	23	20

likely there would be fewer ants attending the scale.

On a spring day (7th November) the number of ants attending scale on each of eight trees was counted at approximately two-hourly intervals from 6.00 a.m. until 8.30 p.m. Figure 4.6 shows the mean number of ants per tree at different times during the day. A bimodal pattern of ant attendance was found with peaks at 10.00 a.m. and 4.00 p.m. This is a pattern similar to that found for ant activity on foraging trails in warm weather (Duncan-Weatherly, 1954; Steyn, 1956).

At the same time, R. ventralis larvae and adults feeding on the scale were counted on these trees and on eight which had no ants (Table 4.6(a)). Although the numbers are small, they indicate a clear nocturnal emergence of larvae on the ant attended trees, whereas larvae were seen throughout the day on populations not attended by ants. Adult coccinellids exhibited a similar trend of nocturnal activity on ant attended populations. On trees where there were no ants, adult coccinellids were seen on the scale during the day but there is also evidence of greater activity at night.

The observations on the coccinellid larvae were repeated on 27th and 28th November when they were more abundant (Table 4.6(b)).

One interesting feature of the ant counts is that on the night of the 7th November the population of scale on tree A6 was the only one to be attended by any number of ants. Of the total of 78 ants on the scale on all eight trees at 8.30 p.m., 75 were attending the scale on tree A6. There were no R. ventralis larvae feeding on or near the scale on this tree, although several were hiding in knotholes in the stem. The data from this tree are discussed in some detail later, as it was the only one on which a large number of immature scale (from reproduction in November) survived.

In two daytime surveys on the 17th and 24th October a total of 25 adult R. ventralis were found on the trees with scale attended by ants, and of these, three were feeding on or were near the scale. On the ant-free trees, 58 adult coccinellids were observed, 33 of which were feeding or near scale. There were thus fewer coccinellid adults on the ant-attended trees (25 compared with 58 on the ant-free trees. $\chi^2 = 6.56$, 1d.f.; $p < .05$). The ants were also very effective in reducing the number of adult R. ventralis feeding.

Despite the fact that fewer adults were seen during the day on ant-attended trees there was no difference in the percentage of living female E. coriaceus with eggs of R. ventralis on ant-attended and ant-free trees (60.1% and 62.2% respectively on 27th October. See 5.3E(b)). This may indicate that adult R. ventralis lay at night.

On trees with scale well attended by ants the adult coccinellids were to be found during the day on the outermost twigs far away from scale, sometimes hiding in curled leaves but often resting in exposed positions. A few fed in an opportunistic fashion on small groups of scale sporadically attended by only one or two ants. They were also commonly found under loose bark on the stem or in crevices where the larvae also hide during the day. As darkness fell the larvae and adult moved up the stem, and the adults moved in from the outer twigs to feed on the scale. Sometimes larvae were seen feeding during the day on colonies attended by a few ants but this was uncommon.

In winter, when ants were frequently absent or in very low numbers even on large scale populations, although some larvae of *R. ventralis* fed openly during the day there was once again a clear nocturnal emergence with the larvae feeding at night at temperatures of about 12°C. Adult coccinellids were seen feeding during the day and also at night in winter.

In summary, larvae and adults of *R. ventralis* fed on unattended scale during the day and at night. On trees with scale attended by ants *R. ventralis* was uncommon during the day, those present resting or searching far away from scale and ants. After dark when the numbers of ants decreased, larvae and adults emerged from hiding and fed.

4.5C Ant attack on *Rhizobius ventralis*

Iridomyrmex sp. B attacked both larvae and adults of *R. ventralis* attempting to feed on *E. coriaceus*. The behaviour of the ants and the predator was examined using larvae of *R. ventralis*. Larvae were used not only for convenience, but also because they are not protected by a hard cuticle (as are the adults) and so are more susceptible to damage by the ants. They are also not as mobile as the adults which, when attacked, move quickly away from the scale colony and the attacking ants, or press themselves onto the branch and so present a hard, smooth, hemispherical shell which foils the ants' attack.

The ant-coccinellid larva interaction was examined just after dawn, at midday and at night. As the interaction was vigorous and clear-cut, only five third and fourth instar coccinellid larvae were used for each trial. Larvae were placed near colonies well attended by ants (about 5-10 ants per 50 scale) and the reactions of the ants and larvae were observed as the latter approached the scale colony. Five similar larvae were placed on an ant free colony to act as a control.

a. Dawn on a cool morning (temperature 11.1°C)

The ants were sluggish and there was no traffic on the stem of the tree. They did not attack any of the larvae which were placed close to the colony, but examined them persistently. Within 10 minutes, four of the five larvae left the colony and were searching the stem of the tree, hiding in crevices and under bark. One larva remained very still near the scale colony and was not attacked during the first hour of observation; it disappeared soon afterwards. The larvae on the control tree were still on the colonies after 15 minutes but one later moved down the stem. The other four remained on the colony and were removed after one hour.

b. Noon (22.3°C)

The ants were active and aggressive. All five larvae were attacked and driven away from the scale, one to a distal twig, three dropped off, and one fell off carrying the attacking ants with it. The five larvae on the control tree began feeding and moved very little in the course of the observations.

c. Night. 8.00 p.m. (16.2°C)

Once again all five larvae were attacked and either dropped from the tree or were driven away from the colonies. The five larvae on the control tree stayed and fed.

When the larva first encounters ants it stops moving and remains perfectly still. If there is a lull in the ants' activity the larva moves quickly away, stopping when it encounters ants again. The ants often lose interest once the larva stops moving and usually go away. If there are few ants attending a small colony of scale, a coccinellid larva often moves far enough away in this stop-start manner to get out of the sphere of activity of the ants altogether and finds an isolated leaf where it remains.

When the ants attack more seriously by biting and stinging, the larva releases a red repugnatorial secretion from dorsal glands on the abdomen. The red viscous fluid may adhere to the ants' mandibles (which the ants wipe repeatedly on the bark of the tree) and may also adhere to the antennae and legs. Banks (1962) and Bartlett (1961) report similar reactions of ants to these secretions. When a larva is attacked by a large number of ants these secretions are of little protective value; they may be useful however if there are only one or two ants attacking. After a severe attack the larva may drop from the branch and often does so when it has just experienced an attack but is not actually being attacked. This is possibly an escape reaction. None of the larvae on the control trees dropped from the twigs. Furthermore, in the laboratory, a larva will often firmly adhere to the substrate (using its pygidial area). Therefore it seems unlikely that they dropped off the twigs after they had been attacked by ants, but while they were not actually being attacked, purely by accident. Bradley (1973) also found that adult coccinellids (_Hyperaspis congressis_) dropped from the branches when attacked by ants.

If present in some numbers, ants can thus protect scale at all times of the day from attack by larvae of *R. ventralis*. Larvae have some chance of remaining near the scale and feeding only if the number of attendant ants is small.

Camponotus sp. encountered larvae of *R. ventralis* at night but took no notice of them. These ants were present in small numbers and so no conclusions can be reached on their protective effect.

4.5D Significance of the protective effect

Nixon (1951) concluded that ants may accidentally disturb the natural enemies of the homoptera they attend or that they are naturally hostile to erratic moving objects and the protection they give the homoptera they attend is thus incidental. Way (1963) gives much evidence to show that this is not entirely true, as ants have been shown to demonstrate ownership behaviour and are aggressive to organisms which are normally ignored if these intrude onto the territory where ants are collecting honeydew from homoptera (El-Ziady and Kennedy, 1956). It has been demonstrated that when honeydew is in short supply ants are more aggressive at their food source and hence protect the homoptera to a greater degree (Way, 1954).

Ants attending *E. coriaceus* probably do not recognize *R. ventralis* as a specific threat because they attack any moving object near the colonies they are attending. When aphids and larvae of *Tribolium castaneum* were placed on colonies attended by ants, they were removed. Some coccinellid larvae (*Diomus* sp.) seemed to be tolerated, however, and this is possibly due either to the waxy covering on their dorsal surface or to their slow movement.

The ants reacted differently to larvae of *R. ventralis* on different parts of the tree. This seemed at least partly due to different behavioural states of the ants when they were attending scale and when they were further away. Five larvae of *R. ventralis* were placed in the stream of ants moving on the stem; although all encountered the ants, none was attacked. This was in marked contrast to the aggressive behaviour demonstrated at the scale colonies. On the other hand, the ants on the stem quickly attacked and captured larvae of *T. castaneum* in the same situation, indicating that they were, even on the stem, aggressive and capable of attacking moving objects. The high rate of capture of *T. castaneum* was almost certainly due to the behaviour of the larvae which wriggled vigorously when examined or attacked, and capture by the ants was then immediate. The larvae of *R. ventralis*, however, remained perfectly still until the ants stopped examining them and then moved slowly out of the stream of ants, evidence once again of their behaviour being suited to an existence with ants. The number of encounters before *R. ventralis* larvae reached safety and before *T. castaneum* larvae were captured are shown below.

Trial No.	*Rhizobius ventralis*	*Tribolium castaneum*
1	11	1
2	10	3
3	33	1
4	23	2
5	6	2

4.5E Influence of ants on the survival of larvae of *R. ventralis* and *Chrysopa ramburi*

The discussion so far has centred around the protective influence of the ants on the scale. It seems likely that the attendance of the ants reduced the population of larvae of *R. ventralis* and *C. ramburi*. To see if this was so the following simple experiments were performed.

Ten potted trees were seeded with scale. A piece of corrugated cardboard was tied around the base of each tree to simulate bark and provide a shelter for *R. ventralis* larvae. Five third or fourth instar larvae were seeded onto each tree. The trees were divided into two groups and placed outside the glasshouse; one lot stood on the ground and the other on inverted pots in basins of water (to prevent ants tending the scale). After five days the trees were again examined. On the ant-free trees, 18 larvae were found but on the ant-attended trees there were only 4 larvae; the differences between treatments were significant ($\chi^2 = 4.45$, 1d.f.; $p < .005$). The missing larvae could not be found in the pots and had obviously left or been killed by the ants.

A similar experiment was performed with *Chrysopa ramburi*. Five eggs of *C. ramburi* were placed on each of 10 potted trees infested with scale in a glasshouse. Ants were allowed to tend five trees. After 7 days there were 15 larvae on the ant-free trees but none on the ant-attended trees.

Ants can thus significantly reduce the numbers of larvae of *R. ventralis* and *C. ramburi*.

4.6 Survival of the nymphs of *E. coriaceus* produced by the females studied in 4.3

Although satisfactory results had been obtained by examining the survival of the female scale in the experiment described above it soon became apparent that a study of the survival of the nymphs they produced would even more clearly demonstrate the benefits of ant attendance.

A survey was made of the immature scale surviving one week after the females began reproduction. The areas covered by nymphs were measured and the number of young estimated as described in 1.6D. Attention was restricted to trees which initially had high populations of female scale.

The numbers of young in populations tended by ants ranged from approximately 1,400 to 34,000 whereas on unattended populations the range was 0 to 2,000.

The number of nymphs of *E. coriaceus* present on 27th November

Ants Present		Ants Absent	
Tree No.	Estimated No. Nymphs	Tree No.	Estimated No. Nymphs
A6	34,000	NA6	0
A7	2,000	NA7	0
A8	3,000	NA8	0
A9	1,400	NA9	50
A10	3,700	NA10	2,000

On the unattended trees larvae of *R. ventralis* were feeding continuously on the colonies of immature scale which were destroyed almost as soon as they settled (see 5.3E(c) for the number of coccinellid larvae trapped). By early December all adult females and nymphs on the unattended trees had been completely destroyed. Examinations of the trees in December and January confirmed these findings for no living scale were seen.

On the trees attended by ants, few larvae of R. ventralis were seen during the day, as has been previously described, and the larvae emerged at night in the absence of ants, to feed. Three of the five populations (A6, A8 and A10) were well attended during the day (the other two populations being poorly attended) but only one population (A6) was heavily attended by ants at night (discussed in next section). On one tree (A7) the population of scale was widely spread and observations by torchlight were impossible. Data from the other four trees are discussed.

On tree A6 a total of only four coccinellid larvae were seen in numerous nightly examinations in late November and early December, and then only when there were few ants. On the other three trees examined, numbers of coccinellid larvae were seen.

The nymphal scale on these trees were confined mainly in the lower branches in large colonies (89% of all nymphs on tree A8, 76% on tree A9, and 86% on tree A10). These colonies were extremely vulnerable to attack by coccinellids because they encountered the scale immediately they emerged from beneath the bark. The survival rate of nymphs in such colonies was negligible as they were densely packed and the larvae moved systematically over them feeding. The remaining nymphs were distributed

The number of larvae of *R. ventralis* emerging at night to feed on trees attended by ants during the day.

Tree	No. coccinellid larvae on night of 27th November	No. coccinellid larvae on night of 28th November
A6	1	0
A8	1	2
A9	10	8
A10	5	4

in smaller colonies on the upper branches of the trees and many of these survived.

One of the reasons that these colonies survived on the ant-attended trees and were destroyed on the unattended trees may have been that on the unattended trees coccinellids were free to roam over the tree, day and night, and when a small colony was encountered they stayed near it until it was destroyed completely whereas on the ant-attended trees coccinellids went into hiding during the day and had to search the entire tree again at night. Thus the chance of them finding a small colony again was not great. On one tree poorly attended by ants (A9) a coccinellid larva remained during the day near a small colony of scale which was duly destroyed and the population on the tree extinguished. In early December some of these small colonies were tended by ants at night and these may also have helped to preserve the scale even though ants were present in very low numbers.

TABLE 4.7(a) Total number of ants attending scale at 9.30 p.m.

Date	3.xii.1972	4.xii.1972	5.xii.1972	6.xii.1972	7.xii.1972	8.xii.1972	9.xii.1972
Tree No.	Number of ants attending scale at 9.30 p.m.						
A6	189	716	877	464	116	160	384
A8	8	9	7	10	7	45	7
A9	0	0	0	10	3	5	8
A10	9	23	20	26	24	5	65
A11	0	13	15	9	2	-	4

TABLE 4.7(b) Influence of weather on ant attendance. Counts of ants at 9.30 p.m. on A6. Weather data recorded 9.30 p.m., weather station W.A.R.I.

Date	No. Ants	Temp. °C X_1	Wind Speed Km.p.h X_2
30.xi	292	21.1	29.0
1.xii	82	24.4	41.8
2.xii	905	27.8	16.1
3.xii	189	15.6	48.3
4.xii	716	22.2	35.4
5.xii	877	27.2	22.5
6.xii	464	16.1	11.3
7.xii	116	11.7	11.3
8.xii	160	14.4	11.3
9.xii	384	16.1	11.3

TABLE 4.7(c) Analysis of variance for multiple regression.

Source of variation	Sum of squares	d.f.	Mean square	F
Total	878,904.50	9		
Regression due to X_1	425,999.738	1	425,999.738	7.525*
Deviation from simple regression	452,904.762	8	56,613.095	
Additional regression due to X_2	4.557	1	4.557	.0001 N.S.
Deviation from multiple regression	451,470.390	7	64,495.770	

* $p < .05$

By mid-December all the populations on ant-free trees had been completely destroyed by coccinellid larvae which then left the trees in large numbers. The coccinellid population in the entire area collapsed; this is discussed in more detail in the next Chapter.

Of the trees which had scale attended by ants, eight had populations of scale and females of the second generation began to settle. The observations were concluded at this time because *R. ventralis* had virtually disappeared (only one larva and one adult were seen on the trees examined).

4.7 Factors influencing nocturnal attendance by *Iridomyrmex* sp. B

Under some conditions *Iridomyrmex* sp. B were active at night. Because this nocturnal activity protects populations of scale, attempts were made in November and December to determine the factors which influenced the numbers of ants attending scale at night.

One count was made each night of the number of ants attending scale on each of five trees at 9.30 p.m. from 3rd December to 9th December 1972 (Table 4.7(a)), and attempts were made to correlate these counts with weather data. Four of the populations used were those which initially had large numbers of female scale attended by ants (A6, A8, A9 and A10). The scale had reproduced and the ants were tending both the surviving females and the nymphs they had produced. On one tree (A7) the population of scale was scattered and difficult to find by torchlight, therefore another nearby population also attended by ants was used (A11). On one tree (A6) counts started on 31st November and were completed on 9th December.

On four of the trees (A8, A9, A10, A11) weather seemed to have little influence on the number of ants attending the scale. Temperature is often correlated with ant activity (e.g. Steyn, 1956) but when the number of ants attending scale on these trees was plotted against temperature no trend was apparent. The numbers of ants were highly variable. The reason for this erratic behaviour by the ants was not discovered, but may be partly due to the small populations of nymphs on these trees or to the fact that the colonies of nymphs on these trees were depleted from day to day by predation by coccinellids. If the data for 3rd December is examined it can be seen that once again the number of ants attending increased as the number of scale increased, for tree A6 obviously had the largest population of nymphs, then A10 and A8, with few on trees A9 and A11.

On tree A6 there was strong evidence that temperature at least might influence ant attendance. Often at night strong winds blew down from the hills in the east (this is a characteristic feature of the weather at the Waite Agricultural Research Institute); I thought this factor might also be important. Counts of ants on tree A6 were continued for only ten nights as during this time predator moth larvae (<u>Catoblemma</u> sp.) were starting to destroy the colonies of scale and thus the most important base variable, i.e. the number of scale, was also changing slowly. Over the period of observation the number of scale on this tree declined slowly. With only ten values for the dependent variable I used only two independent variables (temperature and wind speed at 9.30 p.m., see above) for the multiple regression. Table 4.7(b) shows the influence of these factors on ant attendance and analysis indicates that only temperature has any significant influence on the number of attendant ants (Table 4.7(c)).

When I was searching for R. ventralis one night in late January 1973, night temperatures of 25°C were common and the colonies were swarming with ants (there were no R. ventralis). In July 1973 when daily maximum temperatures were only about 15°C, ants were sometimes completely absent or present in very small numbers even during the day (especially when it was raining).

Some explanation must be sought for the unusually large number of nymphs produced and surviving on tree A6 and for the collapse of the population on tree A10. On the 27th November the numbers of nymphs on the trees were 33,950 and 3,700 respectively. Both trees initially had large populations of female scale with high survival rates at the time of reproduction (1,147 and 1,348; 37.1%, 49.2% respectively). There were basically two reasons for the high survival rate of nymphs on tree A6. Several nightly inspections in early November showed that even before immature scale were produced, scale on tree A6 were more likely to be attended at night by ants than scale on any of the other trees. The reason for this is unknown; it may be that this tree was near a large nest or trail but as the entire area was covered by nests and trails this was difficult to verify. Tree A10 had a lot of loose bark on the branches and the stem, whereas tree A6 was remarkably smooth. Coccinellids could thus hide close to the scale on the former tree and an inspection under the bark revealed large numbers of larvae. On tree A6 larvae could hide only in several knotholes on the stem, and this coupled with frequent attendance by ants at night ensured the survival of a large scale population.

The amount of loose bark on a tree was therefore very important to the survival of the scale for it provided hiding places for larvae and adults of *R. ventralis*. This may have been one of the main reasons for the difference in population trends between Obs. 1 and Obs. 2 from November 1971 to January 1972. The former tree had almost no loose bark, and very few coccinellid larvae. The population increased from 14,900 to 21,600. The latter tree had a lot of loose bark. There were many coccinellid larvae and the population declined from 30,200 to 1,100. (See 1.6F).

4.8 Discussion

Attendance by *Iridomyrmex* sp. B did not increase the rate of development, or fecundity of *E. coriaceus*. The scale derived negligible benefits from the removal of honeydew and the ants did not transport the scale.

The attendance of ants both during the day and at night was important for the survival of the scale. Large numbers of scale attracted large numbers of ants. Ants in large numbers protected the scale from predation by coccinellids. This is very well demonstrated by Figure 5.5 showing the relationship between initial numbers of female *E. coriaceus* and percentage killed by coccinellids. The slope for the ant-attended populations is much steeper than that for the unattended populations. Although the data show that scale in small populations were not protected from coccinellids by the attendance of ants, nevertheless the attendance of ants greatly increased the chances of a few scale surviving. How they did it is not known.

The importance of the amount of loose bark on a tree became evident in November. Where there was a lot of loose bark, larvae of R. ventralis hid beneath it during the day and emerged at night to feed. There was evidence from one population that ant attendance was directly related to temperature and as this is a well known characteristic of ants I think the following comments can be made. Although temperatures in late spring are increasing, cold nights occur e.g. in the last 15 days of November 1972 the temperature at 10.00 p.m. was 10-14°C on 5 nights, 15-19°C on 3 nights, 20-24°C on 4 nights and 25-29°C on 3 nights. When a cold night occurs few ants attend the scale and the coccinellid larvae emerge from beneath the bark to feed; they reduce the scale population which in turn attracts fewer ants and is even more vulnerable to predation. If there is no or very little loose bark there are few coccinellid larvae (as there are no hiding places for them) to reduce the scale population.

In late January temperatures at 10.00 p.m. are high e.g. in the last 15 nights in January 1973 the temperature at 10.00 p.m. was never between 10-14°C, was between 15-19°C on one night, 20-24°C on 5 nights, 25-29°C on 5 nights and 30-35°C on 4 nights. Ants tend the scale more frequently than in November and R. ventralis can not feed.

That the ant/scale ratio for small populations of scale was not greater than that for large populations is really not surprising for the ants are reacting to scale purely as a source of food and one would expect most ants at the strongest source. Where a highly specific relationship exists or where ants are poorly distributed or not abundant e.g. in cool climates, it is no doubt true that the ant/homoptera ratio for large populations of homoptera will be less than that for small populations for the population of ants which have access to the scale is likely to be small. *E. coriaceus* however is attended by many species of ants, particularly species of small *Iridomyrmex* which are both widespread and abundant (Table 4.1(a)). Within a day or two of the seeding of colonies of scale at both the Waite Institute and in Kuitpo Forest the scale were well attended by ants. In the experimental area *Iridomyrmex* sp. B was not territorial (territorality is common in ants; Wheeler, 1910; Wilson, 1963) and all colonies were joined by tracks. The population of ants was extremely large and ants moved quickly over the whole area. Thus even the largest populations I used were well attended. The numbers of scale used were within the range of populations normally encountered and very rarely would the population of scale in the area exceed the ants' capacity to tend them.

Although the ants protected the scale from predation by *R. ventralis* they had little influence on some of the other predators. Some comments on the adaptations of the other predators to deal with the attendant ants will be discussed in the next chapter.

TABLE 5.1(a)

The natural enemies of *E. coriaceus* recorded in this study.

NEUROPTERA

Chrysopa ramburi Schneider (Chrysopidae)

COLEOPTERA

Bucolus fourneti Muls. (Coccinellidae)

Diomus notescens (Blkb.) "

Diomus pumilo Wse. "

Diomus sp? flavifrons Blkb. "

Leis conformis (Boisd.) "

Rhizobius sp. "

Rhizobius ventralis Er. "

DIPTERA

Melangyna (*Austrosyrphus*) sp. near *demastor* (Walker) (Syrphidae)

Pseudoleucopis beneficia Mall. (Chamaemyiidae)

LEPIDOPTERA

Catoblemma mesotaenia Turn. (Noctuidae)

Catoblemma dubia (Butl.) (Noctuidae)

Stathmopoda melanochra Meyr. (Stathmopodidae)

Cyclotorna sp. near *egena* Meyr. (Cyclotornidae)

HYMENOPTERA

Aphycopsis (2 species (Encyrtidae)

HYPERPARASITES

Miocnema sp.
Cheiloneurus sp.
Quaylea sp.

TABLE 5.1(b) The natural enemies of *E. coriaceus* recorded from other sources and where they were found.

COLEOPTERA			
Cryptolaemus montrouzieri Muls.	(Coccinellidae).	Kirk (1908).	New Zealand*
Orcus chalybeus (Boisd.)	"	Kirk (1908).	New Zealand*
DIPTERA			
Pseudoleucopis sp.	(Chamaemyiidae).	Dumbleton (1940).	Hobart
Pseudoleucopis sp.	"	D. Colless (pers. comm.).	Adelaide
LEPIDOPTERA			
Crebota coccophthora Turn.	(Pyralidae)	D.P. Sands (pers. comm. 1969).	N.S.W.
HYMENOPTERA			
Metaphycus sp.	(Encyrtidae)	Dumbleton (1940).	Adelaide.

* Both species of coccinellids originally came from Australia where they probably also feed on *E. coriaceus*.

CHAPTER 5

The natural enemies of *E. coriaceus*

5.1 Introduction

During the course of the study sixteen species of entomophagous insects were seen attacking *E. coriaceus* (Table 5.1(a)). At least three species of hymenoptera known to be hyperparasites as well as several other unidentified species (of hymenoptera) were reared from the scale. Two species of spiders were collected from caged trees on which they were apparently feeding on scale. Two species of mites, one phytophagous and one predatory, were collected from colonies of scale.

Natural enemies of *E. coriaceus* recorded from other studies are shown in (Table 5.1(b)). *E. coriaceus* has a wide geographical range in eastern Australia and Tasmania (Hoy, 1963) and is doubtless prey for many other species of entomophagous insects.

In the following chapter various aspects of the biology of the predators and parasites are discussed. Information on their seasonal occurrence came from sampling the populations of female scale described in Chapter 3.

5.2 Neuroptera: Chrysopidae: *Chrysopa ramburi* Scheider

Chrysopa ramburi has a life history typical of the chrysopidae (Clausen 1940).

The eggs are laid singly or in groups on trees infested with *E. coriaceus* and also on trees which have no or very few scale. In October 1972 large numbers of chrysopid eggs were laid on the experimental plot

TABLE 5.2 The distribution of the eggs of *Chrysopa ramburi* (October 1972).

Number of eggs per tree n.	Number of trees with n. eggs		χ^2
	Observed	Expected (Poisson)	
0	33 { 26	10.32 { 2.83	49.84
1	7	7.49	
2	0	9.92	9.92
3	2	8.76	5.22
4	0	5.80	5.80
{ 5 & above	(5) 1	5.20 { 3.08	≃ .01
6	0	1.36	
7	0	.51	
8	0	.25	
9	0		$\Sigma\chi^2 = 70.79$
10	1		4 d.f.
16	1		
25	1		
37	1		

N.B. Groups have been combined to give expected values greater than 5 - Bailey (1959).

of 40 trees (described in the previous chapter). To ascertain the distribution of eggs trees were searched once as thoroughly as possible (each tree was examined for 5 minutes). The number of eggs laid per tree is compared to the number expected if the eggs were laid in a random manner (Table 5.2). The observed distribution deviates significantly from the Poisson distribution ($\chi^2 = 70.8$; 4 d.f.; $p < .001$) so egg laying is clearly not a random process. Several clumps of eggs were often found on the one tree but on all trees with more than one egg these were laid near, but not usually on, colonies of scale. Of the seven eggs laid one to a tree, two were near scale and the other five far away from colonies.

Adult chrysopids were seen resting on the undersurface of leaves near colonies of scale. They were seen to feed on honeydew; whether they also fed on the larval stages of the scale was not determined. It seems likely that the adults are attracted by honeydew to the vicinity of scale colonies and then lay their eggs, thus ensuring an adequate food supply for their larvae. Hagen and Tassan (1966; 1970) claim that honeydew-like compounds sprayed in fields, attracted _C_. _carnea_ and induced them to oviposit.

The larvae are catholic feeders attacking all stages of _E_. _coriaceus_, some species of aphids, psyllids and other soft bodied insects. They have been seen feeding during the night and in the day also. Even small larvae may attack the female scale, usually turning the head to one side so that only one stylet is inserted deep into the body of the scale. Small larvae usually feed through the caudal opening of the scale.

Larvae of C. ramburi remove the body contents of female E. coriaceus, leaving an expanded, mummy-like shell. The test of the scale is often streaked with the red faecal material of the predators and the test often bears coagulated stains where the stylets penetrated.

Even when there are no definite colonies of homopteran prey the larvae probably stand a good chance of survival because they have great searching abilities. On at least one sizeable tree a chrysopid larva found and destroyed the only two scale on the tree (the larva had pieces of test in its camouflage). It seems possible therefore that very small scale populations may be destroyed by chance as the female chrysopids may lay eggs without encountering scale.

Eggs and larvae were found most commonly in spring each year. In 1971 eggs were laid from September to December and larvae were present until early January 1972. In the spring of 1972 eggs were laid in large numbers from August to November but larvae were not seen on the experimental trees after early November.

Predation by larvae of C. ramburi was secondary in importance to that of R. ventralis. In October and November 1971 the following rates of attack were recorded for C. ramburi and R. ventralis.

Population	% scale killed by C. ramburi	% scale killed by R. ventralis
Obs. 1	4.0%	6.0%
Obs. 2	8.0%	58.0%
Obs. 3	32.0%	68.0%

In September 1972 when nymphs of E. coriaceus were seeded onto experimental trees, some populations were initially attacked by chrysopid larva but in the survey of the 40 trees (previously mentioned) in October 1972 only two chrysopid larva were seen, whereas there were 42 adult *R. ventralis*. (The low survival of larvae was demonstrated as 102 chrysopid eggs were present, mostly recently hatched, but only two larvae were seen). This may be largely due to ants, the presence of which greatly reduced the numbers of chrysopid larvae in an experimental situation (4.6E). Milne (1975) found that when *Iridomyrmex rufoniger* was excluded from trees infested with *Saissetia oleae* the number of chrysopid larvae increased. (Milne, 1975 pers. comm.).

5.3 Coleoptera: Coccinellidae

A list of coccinellids and the stages found feeding on *E. coriaceus* is given below. Most were not commonly encountered, *R. ventralis* being by far the most abundant.

Species	Stage feeding on *E. coriaceus*
Leis conformis	Larva and adult
Bucolus fourneti	Larva and adult
Diomus pumilo	Larva and adult
Diomus sp? flavifrons	Larva and adult
Diomus notescens	Adult
Rhizobius sp.	Adult
Rhizobius ventralis	Larva and adult

Leis conformis adults and larvae appeared in small numbers during

September 1972 (in the experiment on the exclusion of ants, described in Chapter 4) but disappeared from the trees by the end of October. Although they destroyed larval scale during the experiment they were not important predators of *E. coriaceus*. This was the only time during the study I saw them in numbers eating the scale. Furthermore they were obviously not adapted to living with ants. The eggs were laid in an exposed position some distance from the scale; first instar larvae would thus be exposed to the ants before they discovered the scale. The larvae did not demonstrate the avoidance behaviour of *R. ventralis* and were not tolerated by the ants as were the larvae of *Diomus* spp. The decline in numbers of *Leis conformis* in October was almost certainly associated with the increasing attendance of ants on the scale at this time. *E. coriaceus* formed only a small part of the food of this species, for in September and October 1972 the larvae searched widely on the trees, eating aphids and psyllids. *Leis conformis* in fact fed mainly on aphids, especially *Macrosiphum rosae* in a nearby rose bed.

Diomus pumilo and *Bucolus fourneti* appear to be, to some extent, adapted to life with ants. I have seen the larvae of *D. pumilo* feeding in the presence of large numbers of ants both during the day and at night. They are similar in appearance to mealybugs and are covered with long filaments of wax; the pupae are similarly camouflaged. Despite this protection these coccinellids were encountered on only a few occasions and then individually, whereas it was possible to find 20 or more larvae of *R. ventralis* under the bark of some trees. When ants were excluded from scale in September - December 1972, these two species of coccinellids did not increase appreciably in numbers. However, in March 1973 when ants were excluded from some scale populations in an experiment to determine the influence of ants on the parasites of *E. coriaceus*, predation by larvae and adults of *Diomus* spp. caused the failure of the experiment.

Although predatory larvae may be seen feeding on attended scale it should not be assumed that the predators are completely immune to attack from the ants. The ants may cause heavy mortality to these coccinellids in summer but because of their adaptations enough larvae survive to perpetuate the species at a fairly low level of abundance. It is probable that low winter temperatures do not permit the build up of populations of these coccinellids in this otherwise favourable time, when ants are generally inactive. *R. ventralis* is more tolerant of cold conditions and can feed and develop throughout the winter (see 5.3C).

Only adults of *Diomus notescens* and *Rhizobius* sp. were collected feeding on *E. coriaceus* and they were not common.

5.3A *Rhizobius ventralis* Er. Introduction

Rhizobius ventralis is indigenous to Australia and from here it has been introduced into many countries to control scale insects. Koebele took it to California (Essig, 1914), and also to Hawaii (Swezey, 1915); it was introduced into New Zealand (Kirk, 1908), Italy (Martinelli, 1913) and Java, although it did not establish there (Van der Goot, 1921).

R. ventralis feeds on many species of scale insects in California, including *Saissetia nigra* (Smith, 1944), S. oleae (Clausen, 1940), *Coccus hesperidium* (Timberlake, 1913), *Gossyparia spuria* (Herbert, 1924) and the

Figure 5.1

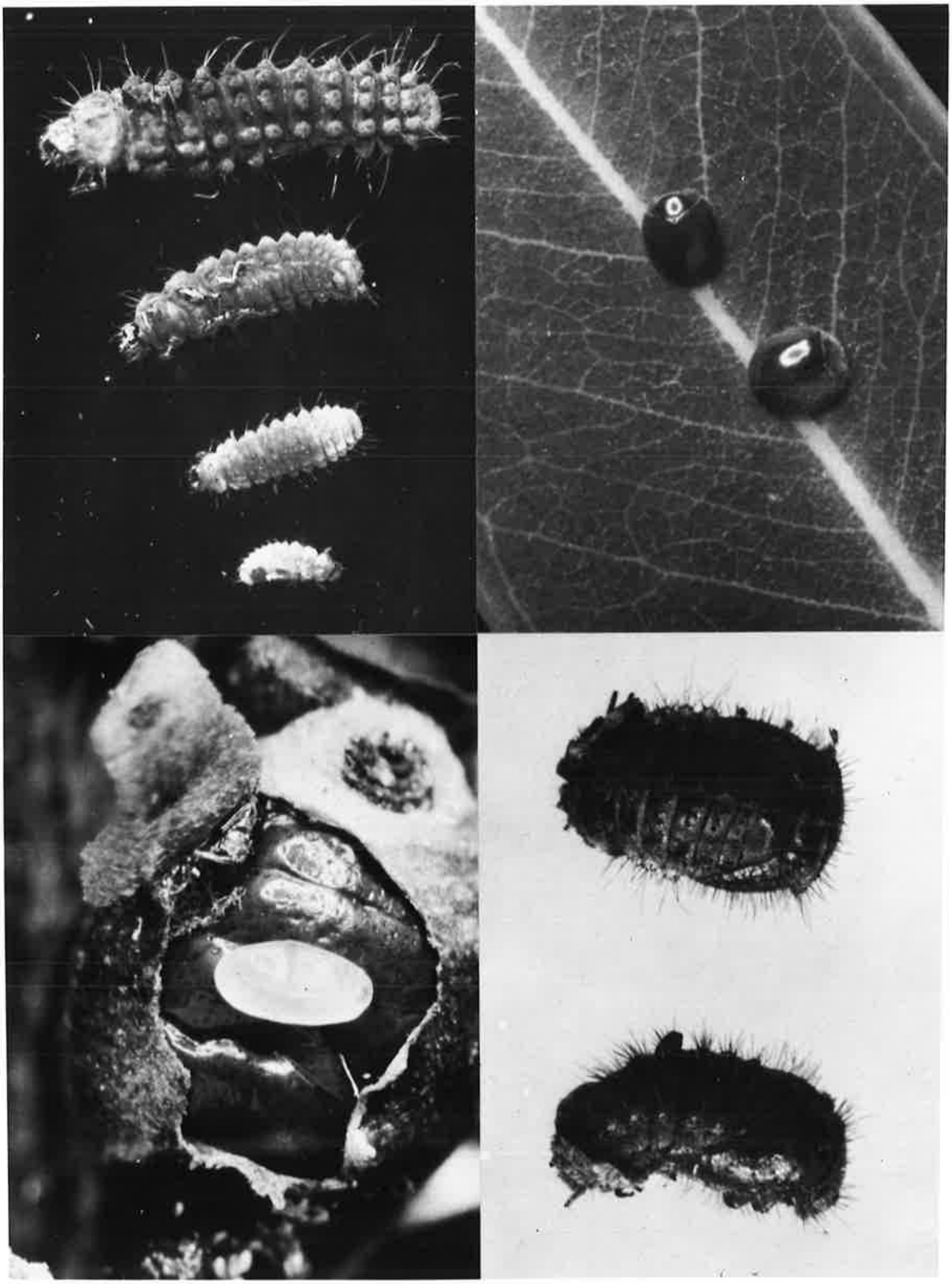
Rhizobius ventralis

Egg x 33 (approx.) Part of the test of a mature female *E. coriaceus* has been removed to show the egg which has been laid on the surface of the body beneath the test.

Larvae x 10 (approx.)

Pupae x 11 "

Adult x 4 "



mealybugs *Planococcus citri*, *Pseudococcus maritimus*, *P. calceolaria* and *P. bakeri* (Essig, 1914). It was introduced into the North Island of New Zealand before 1900 to control *Eriococcus araucariae* on Norfolk Island Pine (Kirk, 1908; Miller, 1924) and from there to the South Island where it was spectacularly successful in controlling *Eriococcus coriaceus* (Kirk, 1908) (see 1.2).

In South Australia I found *R. ventralis* attacking only *E. coriaceus*. It may feed on other native scale but *E. coriaceus*, because of its commonness, must be considered a primary food source. Similarly Froggatt (1907) mentions *R. ventralis* only once and then as a predator of *E. coriaceus*. Host records from specimens in the collection of C.S.I.R.O., Division of Entomology, Section of Biological Control, Sydney, N.S.W. indicate that this coccinellid does attack the introduced coccids *Chionaspis sinensis* and *Gascardia destructor*. Wilson (1960) records *R. ventralis* as attacking *Saissetia oleae*, *Coccus hesperidium* and *Ceroplastes rubens* (all of which are introduced coccids) in Australia.

Despite the importance of *R. ventralis* as an agent in biological control in many parts of the world, remarkably little has been written on its biology. Essig (1914) and Miller (1924) both figure the larva, pupa and adult, but both make few comments on its biology. The standard works on biological control such as Sweetman (1958) and de Bach (1964) merely mention the control of *E. coriaceus* by *R. ventralis* in New Zealand.

In the following sections the biology of the coccinellid as it relates to *E. coriaceus* is described.

5.3B The life history of *R. ventralis*

a. The egg

The egg is elongate-ovoid. When laid on the surface of the scale it is perfectly round in cross section, but as it is normally laid in the space between the scale body and its test it is usually flattened. The egg is .78 (range .723 - .854) mm long and approximately .33 mm in diameter. The surface of the egg is unsculptured and when newly laid is golden and shiny, becoming paler as embryonic development progresses. Sometimes the female scale continues to secrete her test on the inner surface of the egg, which is thus completely enveloped in a felted sac.

The eggs are laid in sheltered positions, almost invariably on the live female scale, beneath the test of the female, between the test and the body of the scale (Figure 5.1). Eggs may be laid dorsally or ventrally to the body of the female. They are usually laid singly but may be found in small groups of two to four. Eggs may also be laid in empty female tests and, very rarely, in a fully exposed position. Hodek (1973) mentions only one coccinellid (*Chilocorus rubidus*) that lays its eggs beneath the test of the scale, and in this case it is the test of the larval scale. Clausen (1940) however, states that such behaviour occurs in several coccinellids including *R. ventralis* which lays its eggs, in California, in the egg chamber of *Saissetia oleae*.

b. The larvae

There are four larval instars (Figure 5.1) which may be distinguished on the width of the head capsule. Mean widths (and ranges) for the four instars were .276 mm (.254 - .285), .386 mm (.346 - .415), .555 mm

(.500 - .592) and .771 mm (.692 - .816).

The first instar larvae feed on the female scale or on crawlers produced in the ovisac of the female. The first instar larva seldom kills the female scale under whose test the egg has been laid. It often chews its way out through the test and it is thus common, especially in late winter and spring, to see large numbers of living female E. coriaceus with the dorsal parts of their tests destroyed. The coccinellid larvae may moult and complete the second larval instar under the test of the female scale. Clausen (1940) comments that R. ventralis feeds on the eggs and young of S. oleae in a similar fashion. Young coccinellid larvae may escape from, or enter under the test of the female scale by way of the caudal opening.

In trials in which coccinellid larvae were reared at 20°C (75% R.H.) on reproducing female scale for the first two stadia, and on female scale only in the final two stadia, I found that, in common with other coccinellids (Hodek, 1973) the fourth instar larva consumed more prey than the other instars combined. The first instar coccinellids consumed mainly larval scale in these trials but they have also been observed feeding on the exposed bodies of the female scale. Second instars attacked larval scale and mature females. The larvae consumed one to two female scale each (mean 1.2) during the third stadium and four to six female scale (mean 5.4) during the fourth stadium. Overall consumption under these conditions was between six and eight (mean 6.9) moderately sized female scale (2.59 ± .12 mm).

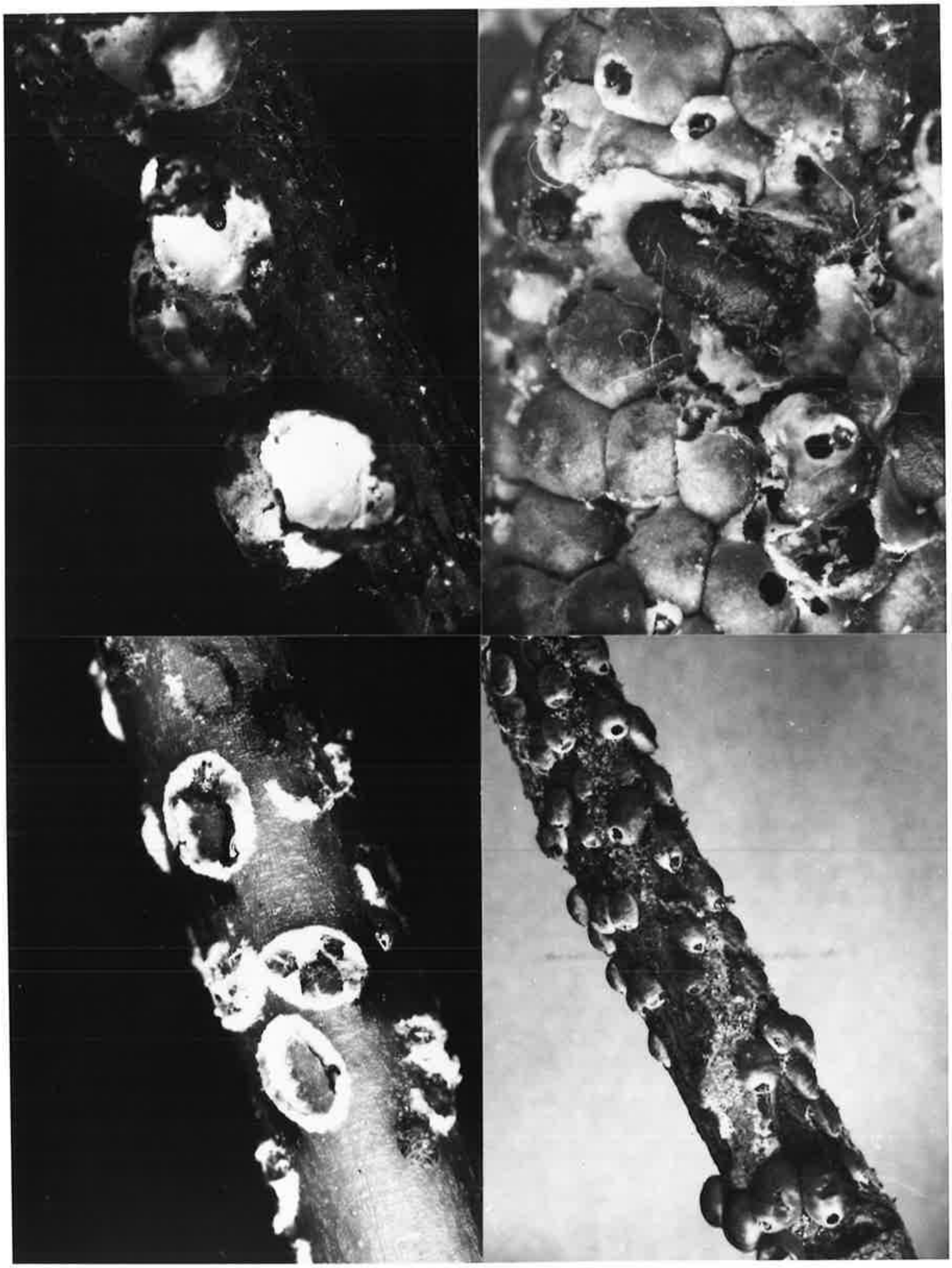
When feeding on a female scale, the first instar larva makes a small

Figure 5.2

Left: Mature (top) and newly settled (bottom) female *E. coriaceus* killed by *R. ventralis*. Note "blood stains" and faecal pellets surrounding the scale and also the ragged holes made by the predators.

Right: (Top) The tests of female scale have been dissected away to show the pupal case of *Pseudoleucopis beneficia*. Exit holes made by hymenoptera (not to be confused with the caudal opening in the test) are also visible.

(Bottom) A silken tunnel made by *Stathmopoda melanochra*.



puncture in the dorsal surface of the scale and imbibes the body fluid of the scale as it flows out. If the larva is removed from the scale the "blood" coagulates over the wound and the scale continues to live. This was apparent from an examination of scale in the field, where many had quite old "blood stains" and yet when dissected contained body fluid and eggs in an apparently good condition.

The appearance of female scale destroyed by _R. ventralis_ is quite characteristic (Figures 5.2(a) and 5.2(b)). Ragged holes are chewed in the test and sometimes the body of the female scale remains shrivelled up in the test. Red-brown stains are evident around the mutilated areas of the test and the red-black faecal pellets of the coccinellids are found on the scale and on the twig nearby.

Cannibalism is not common among larvae but they sometimes eat one another if food is short.

c. The pupa

The mature fourth instar larvae hide beneath loose bark on the stem of the tree and fix themselves to the substrate by using the "anal organ". They enter a prepupal stage which lasted for several days at 20°C. As in other coccinellids, the larval skin is shed and remains encircling the caudal (attached) end of the pupa.

The pupae were 4.34 mm (SD .15 mm) long and 2.63 mm (SD .15 mm) wide (at the widest part). These measurements are for 12 pupae of both sexes reared under optimal conditions (unlimited food; temperature 15°C).

d. The adult

The adults of both sexes produced from larvae and pupae reared at 15°C were 4.18 mm (SD .28 mm) long and 3.01 mm (SD .27 mm) wide (greatest width). Adults reared at higher temperatures were smaller. The newly emerged adult is a rich orange colour, apart from the head, thorax and legs which are black or dark brown. The elytra blacken in about 2-3 hours at 20°C. The adults initially remain near the pupal skin, sometimes for up to 24 hours after emergence.

The defensive secretion of the adults is pale yellow.

At 20°C (75% R.H.) the adults began feeding and mating one to two days after emergence from the pupa and eggs were laid after about four days. Under these conditions adults consumed 0-4 female scale per day and the mean consumption was 1.7 (mean size of scale 2.44 mm).

Ten adults (both sexes) lived for at least 90 days at 20°C. During this time food was not always readily available (as the supply of scale from the field was erratic) and no records of overall food consumption or the number of eggs laid were made. However, after 70 days, females (which had been mated only at the beginning of the observations) were still laying viable eggs.

5.3C Rate of development of *R. ventralis*

Because the eggs are laid under the test of the female scale and the young larvae feed under the test or in the ovisac, observations on the rate of development of eggs and larvae were somewhat difficult. The following approximate times for rate of development are given. The egg stage lasts for six to seven days at 20°C and 12 to 15 days at 15°C. The mean times for larval and pupal development are shown below. Five to ten larvae or pupae were used for each determination.

Mean time and range (days) taken to complete development at temperatures shown.

Temperature	15°C ± .5	20°C ± 1.0	25°C ± .5	30°C ± .5
Time for larval development	36.1(34-41)	21.5(20-22)	15.9(14-17)	14.8(13-17)
Time for pupal development	12.6(12-13)	8.0(7-9)	5.1(5-6)	4.2(4-5)

There was some mortality in the pupal stage at 30°C; one of the eight pupae failed to emerge and one adult which emerged had a malformed abdomen. At the lower temperatures there was no mortality.

The life cycle (egg to adult) was completed in about 60-65 days at 15°C. There has been little work done on the rate of development of indigenous (Australian) species of coccinellids but there is some evidence that *R. ventralis* is able to develop at temperatures which are generally unfavourable for other species. Kirk (1908) comments on the cold-hardiness of *R. ventralis* which survived the winter in the South Island of New Zealand whereas *Orcus chalybeus* and *Cryptolaemus montrouzieri* (also Australian species) failed to become established. Readshaw (pers. comm. 1974) working on native *Stethorus* sp., Maelzer and Coleman (pers. comm. 1974) working on *Leis conformis* and *Coccinella repanda* respectively, all found that the insects had difficulty in completing development at 15°C. Most of the eggs of *C. repanda* and *L. conformis* failed to hatch and those first instar larvae which were produced failed to complete the first moult. There was no difficulty in rearing first instar *R. ventralis* at 15°C.

These differences are reflected in the winter populations of the species. *Coccinella repanda* overwinters as adults (Coleman pers. comm.). *Leis conformis* mainly overwinters as adults although the species can also breed slowly during the winter, but larvae do not appear in large numbers until late September and October (Maelzer pers. comm.). On the other hand all stages of *R. ventralis* were found throughout winter. The eggs hatched, larvae developed and pupated under field conditions. Larvae fed on winter nights when temperatures were approximately 12°C.

5.3D The influence of the size of the female scale on feeding and oviposition by *R. ventralis*

Observations in the field indicated that adults of *R. ventralis* seemed more likely to eat smaller female scale than larger ones. This was particularly obvious in one field population which had been artificially established in the winter of 1973 by several seedings from glasshouse colonies. In late October a storm destroyed part of the cage and *R. ventralis* gained entry. In November there were basically two age-groups of scale on the trees, mature females about to reproduce, and developing females which had consolidated their tests and were just beginning to expand and develop eggs. One tree in particular had approximately equal numbers of mature and immature female scale, and on this tree large patches of developing females had been eaten by the coccinellids

TABLE 5.3 The comparison of the observed distribution of eggs of *R. ventralis* and that expected if the eggs were laid without regard to the size of the female scale (i.e. at random).

Size class x of female scale (mm)	Total no. of scale examined in size class x	No. with coccinellid eggs in size class x		No. expected on a random basis		χ^2
1.83 - 2.13	11	0	4	3.2	12.7	5.96
2.13 - 2.44	33	4		9.5		
2.44 - 2.75	67	12		19.3		2.76
2.75 - 3.07	81	22		23.3		.07
3.07 - 3.37	46	22	31	13.3	16.8	12.00
3.37 - 3.66	12	9		3.5		

$\Sigma\chi^2 = 20.8$

TABLE 5.4 The comparison of sizes of female *E. coriaceus* offered to *R. ventralis* and those eaten.

Size class x of female scale (mm)	No. offered in class x	No. eaten in class x		Expected on a random basis		χ^2
1.23 - 1.51	4	2	33	.2	14.6	23.19
1.54 - 1.81	51	12		3.3		
1.85 - 2.12	170	19		11.1		
2.15 - 2.43	256	15		16.6		.15
2.46 - 2.74	193	3		12.6		7.31
2.77 - 3.05	77	0	0	5.0	6.2	6.20
3.08 - 3.35	20	0		1.3		
3.38 - 3.66	10	0		.9		

$\Sigma\chi^2 = 36.85$

TABLE 5.5(a) Comparison of size of female *E. coriaceus* offered and those in which *R. ventralis* laid eggs.

Size class x of female scale (mm)	No. of scale offered in class x	No. in class x in which eggs were laid	Expected on a random basis	χ^2
1.23 - 1.51	9	0 } 8	2.4 } 14.2	2.71
1.54 - 1.81	44	8	11.8	
1.85 - 2.12	85	25	22.8	.21
2.15 - 2.43	81	20	21.7	.11
2.46 - 2.74	53	17	14.2	.55
2.77 - 3.05	14	6 } 9	3.8 } 5.7	1.91
3.08 - 3.35	7	3	1.9	

$\Sigma\chi^2 = 5.49$

TABLE 5.5(b) As in 5.5(a) but with those samples with only small female *E. coriaceus* not included.

Size class x of female scale (mm)	No. of scale offered in class x	No. in class x in which eggs were laid	Expected on a random basis	χ^2
1.23 - 1.51	8	0 } 3	2.1 } 8.3	3.38
1.54 - 1.81	24	3	6.2	
1.85 - 2.12	50	11	12.9	.28
2.15 - 2.43	57	13	14.7	.20
2.46 - 2.74	40	15 } 23	10.3 } 14.1	5.62
2.77 - 3.05	9	6	2.3	
3.08 - 3.55	6	2	1.5	

$\Sigma\chi^2 = 9.48$

(which were mainly adults) but few of the mature female scale had been eaten.

It was also observed that many of the mature female scale had coccinellid eggs beneath their tests but dissections of immature females revealed few eggs. Five colonies of each were chosen at random from the tree and dissected. The results are shown below.

The influence of the condition of the female scale on the deposition of eggs of *R. ventralis*.

Status of the female scale	No. examined	No. with eggs of *R. ventralis*
Mature females i.e. about to reproduce	250	68
Immature females	204	1

Within the samples of mature scale the eggs of the coccinellids were not distributed randomly with regard to the size of the female scale. From each sample 50 scale were chosen at random, their length measured and the test removed from each scale to see if there were any coccinellid eggs. Table 5.3 shows the combined data for the 250 scale examined. In each sample the proportion of scale with eggs increased as their size increased and a comparison of the actual distribution of sizes of scale containing eggs and that expected if eggs were laid at random (with regard to size of female host) shows them to be significantly different $\chi^2 = 20.8$ with 3 d.f.; $p < .001$. (Note that the first two and last two size classes have been combined in order to give an expected value above five which is necessary for a comparison involving χ^2. Bailey, 1959).

It seemed that female coccinellids laid eggs in larger scale and devoured smaller ones, thus avoiding the obvious difficulty of destroying scale into which eggs have been laid. As the observations were made in the field it was possible that influences other than size of the female scale may have determined where the coccinellids laid eggs, and so laboratory studies were performed as follows:-

Four- to seven-day old adult R. ventralis (of both sexes) were used. The females had mated prior to the experiment. Beetles were individually enclosed in small plastic cages 3 cm in diameter and 1 cm high, the lids having a hole covered with gauze. The beetles were kept at 20 ± .5°C and 75% R.H. Each coccinellid was given 10-20 mature female scale a day and each day the scale were removed, the lengths of those attacked and the lengths of the survivors measured. Each scale was also dissected and examined for coccinellid eggs. Nine beetles were used and the trials continued for five consecutive days.

Table 5.4 gives the distribution of sizes of female scale offered and those eaten. The distributions are dissimilar, the smaller scale being eaten more often by the coccinellids. ($\chi^2 = 36.85$ with 3 d.f.; $p < .001$). Once again, several size classes have been combined (see previous note). If only those samples are considered where scale were eaten (as each coccinellid did not eat scale each day) the same result is obtained ($\chi^2 = 27.54$ with 3 d.f.; $p < .001$).

There was, over the five days, no evidence that eggs were laid in any but a random manner with regard to scale size (Table 5.5(a), $\chi^2 = 5.49$ with 3 d.f., N.S.). The data are in contrast to the field observations and a closer examination revealed the reason. If the combined data from the first four days are analysed alone, the hypothesis that eggs are laid preferentially in larger scale is confirmed (Table 5.5(b), $\chi^2 = 9.48$ with 3 d.f.; $p < .05$). When the results include those from the fifth day they suggest that the eggs are laid independently of scale size. The discrepancy is due to changes in the size range of scale offered to the coccinellids. Because the scale form colonies on twigs it is almost impossible to randomize them for size. All samples in which eggs were laid over the first four days had size ranges from 1.85 mm - 3.08 mm whereas on the fifth day two samples of female scale in which large numbers of eggs were laid had size ranges from 1.54 mm - 2.43 mm. These samples with restricted choice bias the whole results.

Thus female R. ventralis given a wide choice prefer to lay eggs under the test of larger female scale. They will however lay their eggs under the test of small female scale if larger ones are not available.

Besides preventing, as far as possible, adult coccinellids from eating scale into which eggs have been laid, the behaviour described above also ensures that eggs will be laid into female scale which will reproduce soonest and provide crawlers for the first instar coccinellids to feed on.

5.3E Comments on the seasonal occurrence of R. ventralis with observations made in the experiment on the protective influence of ants

This coccinellid was the major cause of mortality in female scale sampled in August and in November and was the most important factor in reducing the high winter populations of scale to the low levels encountered in summer. The impact of the coccinellid on the scale has been examined in Chapters 3 and 4. The major discussion here concerns the population of the coccinellids. Adult *R. ventralis* were used as an index of the population of the species as they were more easily observed than the larvae which have cryptic habits and are often difficult to find in the field.

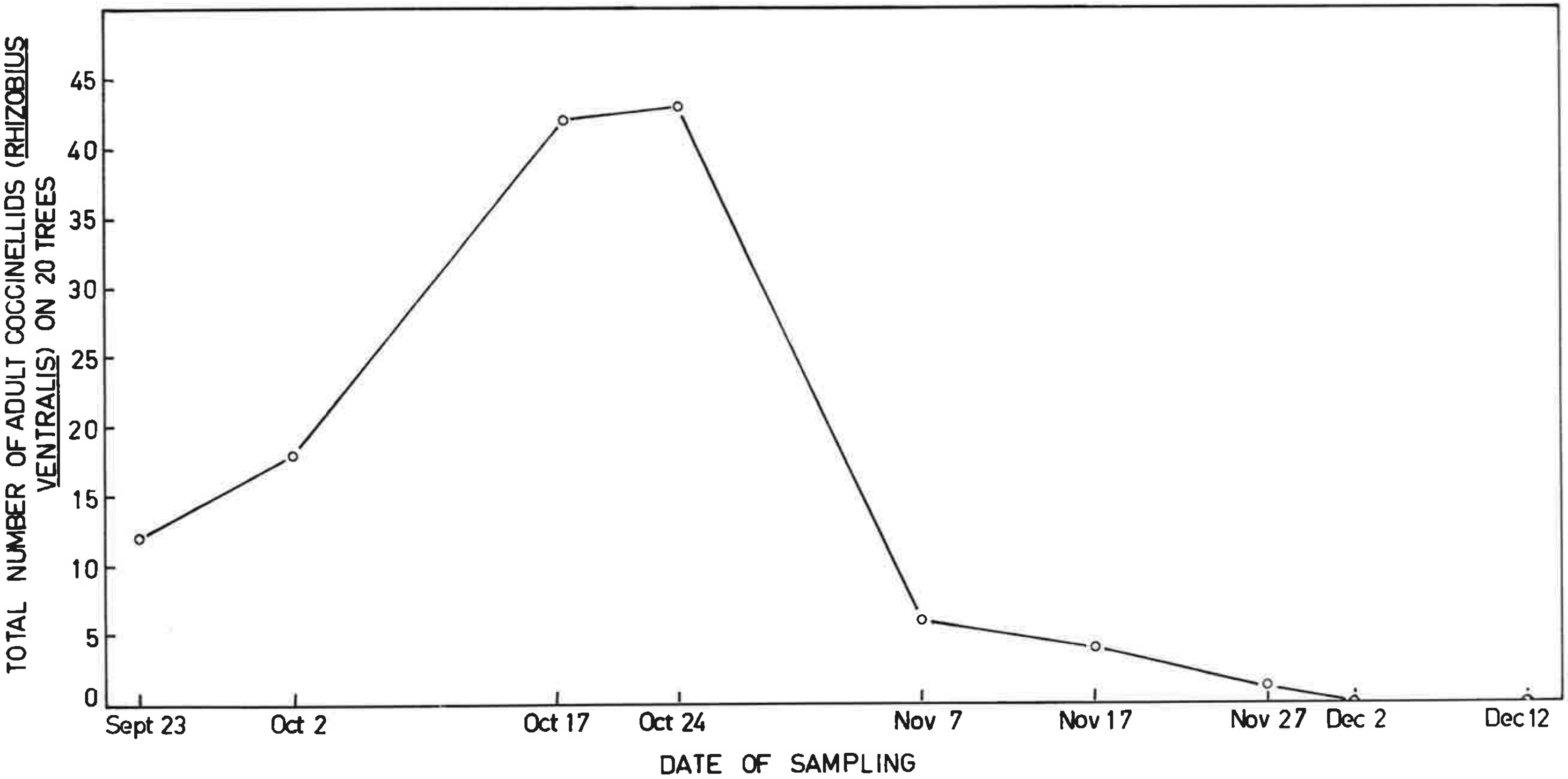
Adult coccinellids occurred in the cooler months, April to November and showed a marked increase in numbers in late spring. The population then declined rapidly and by mid-December and early January in the first year of the study (1971-1972) they were present in low numbers (see 1.6F) and were entirely absent in the second year (1972-1973) (see following pages). By mid-January and through until March in both years none were found but in April isolated individuals again appeared. Thus November was not only a time when the scale population collapsed but the coccinellid population was also greatly reduced. The reasons for the decline in numbers of *R. ventralis* is discussed in relation to the experiment described in Chapter 4.

Whilst the experiment to determine the influence of ants on the survival of the scale was in progress counts were made of the numbers of adult *R. ventralis* present on the 20 experimental trees. As the trends elsewhere in the observational area appeared to be similar, these counts probably provide an accurate picture of the overall trends in numbers of adult *R. ventralis*.

Counts of adult coccinellids were made on all trees at intervals of

Figure 5.3

Trends in the total number of *R. ventralis* on 20 trees (September to December 1972).


TOTAL NUMBER OF ADULT COCCINELLIDS (RHIZOBIUS VENTRALIS) ON 20 TREES
45
40
35
30
25
20
15
10
5
0
Sept 23
Oct 2
Oct 17
Oct 24
Nov 7
Nov 17
Nov 27
Dec 2
Dec 12
DATE OF SAMPLING

approximately two weeks from September to December. An attempt was made to see if adult coccinellids had a diurnal rhythm of activity (so that counts could be made when they were most active). Trees were examined between 7.00 a.m. and 5.00 p.m. (at this time, nocturnal activity was not suspected) and as no pattern of activity emerged, all subsequent counts were carried out beginning at 10.00 a.m. on fine warm days (to avoid any bias due to weather conditions). Each tree was searched for three to five minutes, depending on its size.

The trends in total numbers of adult *R. ventralis* are summarised in Figure 5.3. The population trends of the adults can be divided into three phases:

a. Increase in numbers in mid-October and

b. Subsequent decline in early November followed by

c. Complete disappearance in December.

Each phase will be discussed.

a. The increase in numbers of adult *R. ventralis* in October 1972

Regular counts of adult coccinellids were not made on the three trees from which the experimental stock was taken but only a few adult coccinellids were seen during the sampling of the scale populations in July and August 1972. Large numbers of larvae were seen in September feeding on scale which remained on the trees from which the experimental stock was taken. Emerging adults probably moved to the experimental trees causing the increase in numbers from 17th to 24th October. The peak in numbers of adults occurred about seven weeks after the female scale of the previous generation began to reproduce. This was almost exactly the time it must have taken for the development from first instar larva to adult in the field at that time. The time for combined larval and pupal development at 15°C was 49 days (36 and 13 days respectively; see 5.3C) and the mean daily temperatures at the Waite Agricultural Research Institute during September and October were 14.7°C and 16.1°C respectively.

This may have been coincidence, however on other occasions I noticed that the number of larvae attacking the scale population increased after reproduction by the female scale. There was thus circumstantial evidence that the attack of _R. ventralis_ was synchronized with reproduction of the female scale. Hagen (1962) comments that coccinellids which attack sedentary homoptera frequently synchronize their attack with the reproduction of their prey. Whether this was because more eggs were laid by the coccinellids, or because more larvae survived, is unknown. Perhaps the chance of survival of the first two instars of the coccinellid is increased because they are able to feed on crawlers produced in the ovisac of the female scale. Survival of the second and third instar coccinellid larvae may have increased because the female scale attain their maximum size just before they reproduce and coccinellid larvae can hide in the eaten-out test during the day and emerge at night to feed. Obviously if the scale are small and the coccinellid larvae can not hide in them the larvae must suffer increased mortality near the feeding site and during the trek to and from the resting site under the bark. These speculations, however, remain unverified.

b. Decline in numbers of adult _R. ventralis_ in early November 1972

The cause of the first decline in numbers of adult coccinellids i.e.

the decrease from 43 on October 24th to 6 on November 7th (Figure 5.3) is also uncertain. As the adult coccinellids have a long life, up to three months at 20°C, mortality due to old age can be excluded as a factor in the decline of the population at this time. It seems unlikely that the beetles moved away because of a decline in the numbers of living female scale on the trees, for the survival rate of female scale on many trees was still high e.g. 74.1% and 49.5% on five samples from ant-attended and ant-free high populations on 27th October (see below).

Survival of scale and those survivors with coccinellid eggs. Totals for five samples from five colonies from populations with and without ants in attendance.

Population status	No. scale examined	No. survivors	% surviving	No. survivors with coccinellid eggs	% survivors with coccinellid eggs
Large scale population; ants in attendance	168	120	74.1%	73	60.1%
Large scale population; no ants	182	90	49.5	56	62.2%

The female coccinellids laid many eggs before they disappeared from the experimental trees. Whether they are more dispersive after egglaying, as are some other species, or whether they left the experimental area for another reason, is unknown. Yakhontov (1966) states that even if aphids are plentiful in the cotton fields of Central Asia, adult coccinellids may still leave the fields after laying eggs.

c. The disappearance of adult *R. ventralis*

The decline in activity of *R. ventralis* seemed to coincide with the beginning of hot weather.

In late spring 1971 and early summer of 1971 - 1972, temperatures were below average and rainfall was above normal whereas in late spring and early summer 1972 - 1973 temperatures were normal but there were some hot days in early December and the weather was dry. (Comments from South Australian Year Book, 1973). These differences are apparent in the mean temperatures recorded at the Waite Agricultural Research Institute (Waite Agricultural Research Institute Biennial Report, 1970-1971; *ibid.* 1972-1973).

Mean daily temperatures $(\frac{\text{Max.} + \text{Min.}}{2})$ at W.A.R.I. for the months shown.

	1971 - 1972	1972 - 1973
October	15.4°C	16.1°C
November	16.2°C	18.1°C
December	19.8°C	21.1°C
January	21.2°C	24.6°C

Adult *R. ventralis* were seen on the observational trees from August 1971 until early January 1972 but they were not seen in the second, hotter summer after 2nd December 1972.

There were good reasons for the immediate decline in numbers of *R. ventralis* but the reasons for the numbers remaining low throughout summer are more difficult to understand.

Large numbers of coccinellid larvae hatched from the eggs laid in late October and early November. By late November these larvae had completely destroyed the populations of scale, both females and nymphs, on the trees where ants were excluded. The starving larvae left the trees where they were trapped in the grease bands used to exclude the ants. When the counts below were made some larvae were still on the tree searching for prey.

The numbers of coccinellid larvae trapped and those still on the trees when the large scale populations, unattended by ants, collapsed.

December 1972.

Tree	Total No. Coccinellid larvae trapped	No. 4th instars trapped	Larvae remaining on tree
NA6	0	0	0
NA7	18	0	1
NA8	9	0	3
NA9	10	0	1
NA10	135	20	22

Most of the larvae leaving these trees needed to feed further before they could pupate. Some fourth instar larvae were leaving one tree when they were trapped and it was discovered that all were parasitised by an encyrtid wasp (*Aphycopsis* sp., not the same species as the primary parasite of *E. coriaceus*). The larvae remaining on the trees presumably left soon after these observations were made, as the scale populations were completely destroyed. Thus the fate of all larvae on the trees where there were no ants would have been starvation or death due to parasitism (if they had not been trapped in the grease bands) before they could pupate.

Parasites may play an important part in the ecology of some coccinellid species. Hodek (1973) gives examples of insect (Diptera and Hymenoptera), acarine and nematode parasites of larval, pupal and adult stages of many species of coccinellids. Encyrtids (belonging to the genera _Homalotylus_ and _Tetrastichus_) kill up to 100% of the larvae of some coccinellid species. Rubstov (1954 quoted in Hodek 1973) considers these parasites to be the chief reason for the poor control of coccids by coccinellids of the genus _Chilocorus_ on the Black Seas Coast. Succeeding generations of the coccinellid larvae are parasitized to an increasing degree and by the third generation 90% or more are parasitized thus reducing the number of beetles that enter hibernation and emerge next spring.

The impact of _Aphyscopsis_ sp. on the population of _R. ventralis_ was difficult to assess but was probably not great. Despite the presence of parasites in June and July 1972 the population of coccinellids still increased markedly in the area later in the year. Parasitized larvae were frequently seen in November and early December but at this time the coccinellid population was already adversely influenced by the increased attendance of ants and the shortage of readily available food. The adult coccinellids were also highly dispersive and thus even without a high rate of parasitism the population of _R. ventralis_ would have been greatly reduced.

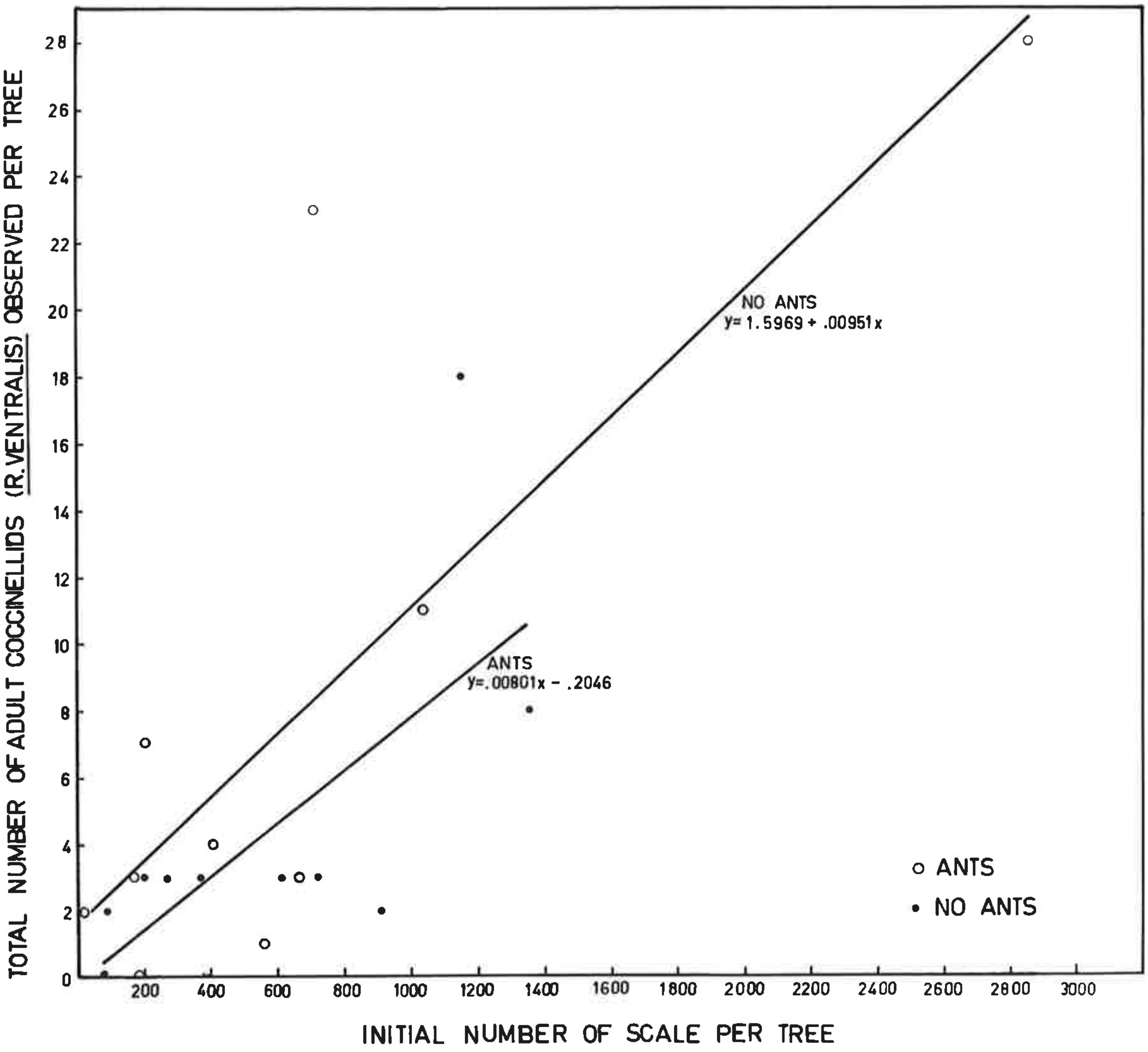
The situation on the trees where the scale were attended by ants was more difficult to assess because the fate of the larval population was not accurately known. The coccinellid larvae were not sampled for parasitism and the loose bark was not removed to count larvae and pupae as I wanted to see the natural outcome of the coccinellid predation on the scale. Many of the younger coccinellid larvae must have died of starvation for the colonies in the lower branches of most trees were quickly destroyed and most of those in the upper branches were not attacked (see 4.6).

Some of the larvae seen in late November were in their late fourth instar and would have pupated. Whilst some were parasitized others must have produced adults. Starvation and parasitism of larval coccinellids, although factors in the decline of the populations of adult *R. ventralis* must therefore be only part of the explanation as a few adults would have been produced from mature fourth instar larvae in late November. Furthermore it must be remembered that the adults are long lived and those which emerged from pupae in October would most likely be still alive in December. Despite careful searching in December and January, under bark near scale colonies and on scale themselves, no adults or larvae of *R. ventralis* were seen. This rarity may be probably due primarily to the presence of ants, both at night and during the day in summer, attending the scale and preventing the coccinellids from feeding. Another possibility (which was not investigated) is that *R. ventralis* has a lower fecundity in summer, a condition found among other coccinellids which live in climates with a hot dry summer (Kehat *et al*., 1970).

It seems that *R. ventralis* is closely adapted to a life with ants. In the area studied prolonged periods of low temperature and rainfall occur in autumn, winter and spring. Both these factors are known to

Figure 5.4

The relationship between initial numbers of female *E. coriaceus* per tree and the total number of adult *R. ventralis* observed in six counts showing the aggregation of the predator.


TOTAL NUMBER OF ADULT COCCINELLIDS (R.VENTRALIS) OBSERVED PER TREE
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
NO ANTS
y= 1.5969 + .00951 x
ANTS
y=.00801x - .2046
○ ANTS
• NO ANTS
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
2600
2800
3000
INITIAL NUMBER OF SCALE PER TREE

inhibit ant activity and although ants may tend the scale in winter they are frequently absent or present in very low numbers. Temperatures of 15°C and below do not prevent *R. ventralis* from feeding and developing. The coccinellid can therefore take advantage of the decline in ant activity in cold weather and feed on the scale. The coccinellid has behavioural patterns for avoiding the attendant ants even in late spring but these are of little use in summer when temperatures are high and ants tend the scale continuously.

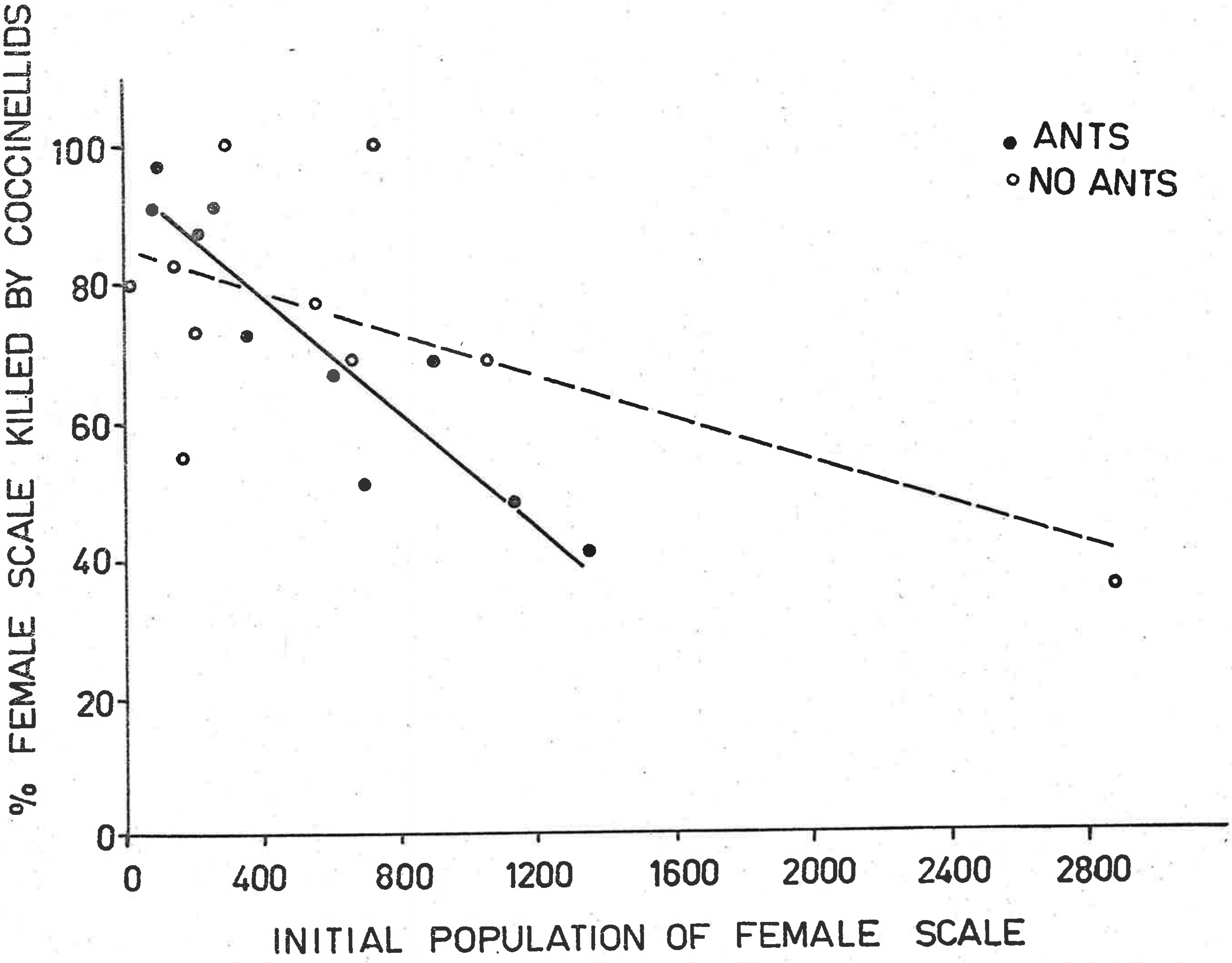
5.3F The relationship between the initial number of scale per tree and the number of adult *R. ventralis*

Predators and parasites aggregate in areas of high density (Hassell, 1968). There may be several reasons for the formation of such aggregations, one of the most common reasons being the change in behaviour of an individual predator once prey is encountered. A searching predator may shorten the length of its steps and increase the frequency with which it turns after it encounters prey(Hassell and May, 1974; see also Banks, 1957; Dixon, 1959). This behaviour leads to an aggregation of predators in areas of high prey density. Adult *R. ventralis* aggregated on trees with large populations of scale.

The linear regression of the total number of adult *R. ventralis* observed on a tree during the period 23rd September to 27th November 1972 on the initial number of scale on the tree was significant (Figure 5.4). For those populations attended by ants $F_{1,8} = 7.284$ ($p < .05$) and for the unattended populations $F_{1,8} = 13.762$ ($p < .01$).

Figure 5.5

The relationship between initial numbers of female *E. coriaceus* and the percentage killed by coccinellids.


% FEMALE SCALE KILLED BY COCCINELLIDS
100
80
60
40
20
0
● ANTS
○ NO ANTS
0
400
800
1200
1600
2000
2400
2800
INITIAL POPULATION OF FEMALE SCALE

5.3G The influence of the size of the population of *E. coriaceus* on the percentage of the scale killed by coccinellids

The regression of percentage of female scale killed by *R. ventralis* on population size is significant for both ant-attended and unattended populations, the percentage decreasing as the initial population size increases (see Figure 5.5). For attended populations $F_{1,8} = 46.712$ $(p < .005)$ and for unattended populations $F_{1,8} = 6.109$ $(p < .05)$. This was despite the aggregation of adults of *R. ventralis* in the areas of high prey density.

The protective influence of ants can be seen in the difference in slopes of the two regression lines; large numbers of ants attended the larger scale populations and protected them more effectively than the small numbers of ants attending the smaller scale populations.

It is tempting to try to interpret the data in terms of Royama's (1971) model for the influence of prey density on percentage of prey killed by predators but the fact that scale were killed by larvae of *R. ventralis* (the numbers of which were not counted) as well as by adults, makes this impossible.

The most striking feature of the data in Figure 5.5 is the efficiency of the coccinellids at low levels of prey density. The adults and larvae obviously had no difficulty in finding scale even when there were very few on a tree. The low percentage of scale killed by coccinellids in the largest unattended scale population is also difficult to explain by current theories on the effect of prey population numbers on aggregation and percentage mortality caused by predators unless one assumes this is a very high prey population which even the aggregative effect of the predators cannot reduce.

The efficiency of the coccinellids at low densities may be partly explained by their searching behaviour and by the nature of the colonies formed by *E. coriaceus*. *R. ventralis* must have considerable searching powers to survive in the wild for populations of *E. coriaceus* are frequently widely dispersed. The trees used were 1.5 m - 2 m high with few side branches. Coccinellids detect their prey only on contact (Fleschner, 1950; Bänsch, 1966); adult *R. ventralis* search in a linear fashion along the twigs. Even in small populations *E. coriaceus* forms colonies which frequently encircle the twig. Thus the chances of such a colony being found by *R. ventralis* was high. Once a colony is encountered the prey density is immediately high and the coccinellid can feed and lay eggs.

5.4 Diptera

5.4A Syrphidae: *Melangyna (Austrosyrphus) sp. near demastor (Walker)*

Larvae were seen feeding on the nymphs of *E. coriaceus* in August 1972 and August and September 1973. This species was of no importance in the ecology of the scale.

5.4B Chamaemyiidae: *Pseudoleucopis beneficia* Mall.

P. beneficia was described by Malloch (1930) from specimens bred from *E. coriaceus*. The egg, larval and pupal stages were described by

Figure 5.6

Pseudoleucopis beneficia

Test of female *E. coriaceus* removed to show the ectoparasitic habit of the larva of *P. beneficia*. It has entirely destroyed the body of the coccid.

Adult *P. beneficia*

Dumbleton (1940) from material collected near Adelaide.

The eggs are laid in crevices between contiguous female scale or on the bark near scale. The first instar larvae enter the test of the female scale presumably via the caudal opening. Once beneath the test the larvae feed as ectoparasites. Larvae are most commonly found singly beneath the test of the scale. A larva normally consumes 1-4 female scale depending on the size of the scale and how easy it is to move from one scale to another. In winter and spring when the female scale are largest, one or two are attacked; in summer when the scale are small and the colony density is high four scale may be attacked.

The family Chamaemyiidae has many members the larvae of which are predatory on aphids and scale insects. Some larvae range widely over the host plant in search of prey, very much like syrphids, and others are modified for a parasitic existence beneath the test of the female scale (Sluss and Foote, 1971; 1973). The third instar larvae of _P. beneficia_ were ectoparasites (Figure 5.6). They were virtually helpless when removed from beneath the test of the female scale and, even in the laboratory, frequently fell from the twig. Indeed it seemed very difficult for large larvae to get back beneath the test of the scale once they were removed. Second instar larvae may move over the twig, and by chewing a hole through the test of a scale, may re-establish themselves. However this process of gaining entry to a new scale was observed once and took about four days and it seems that the larvae rely heavily on scale touching one another in order to move from one scale to another (5.8).

The larva pupates in the last larval skin which is cemented to the

Figure 5.7

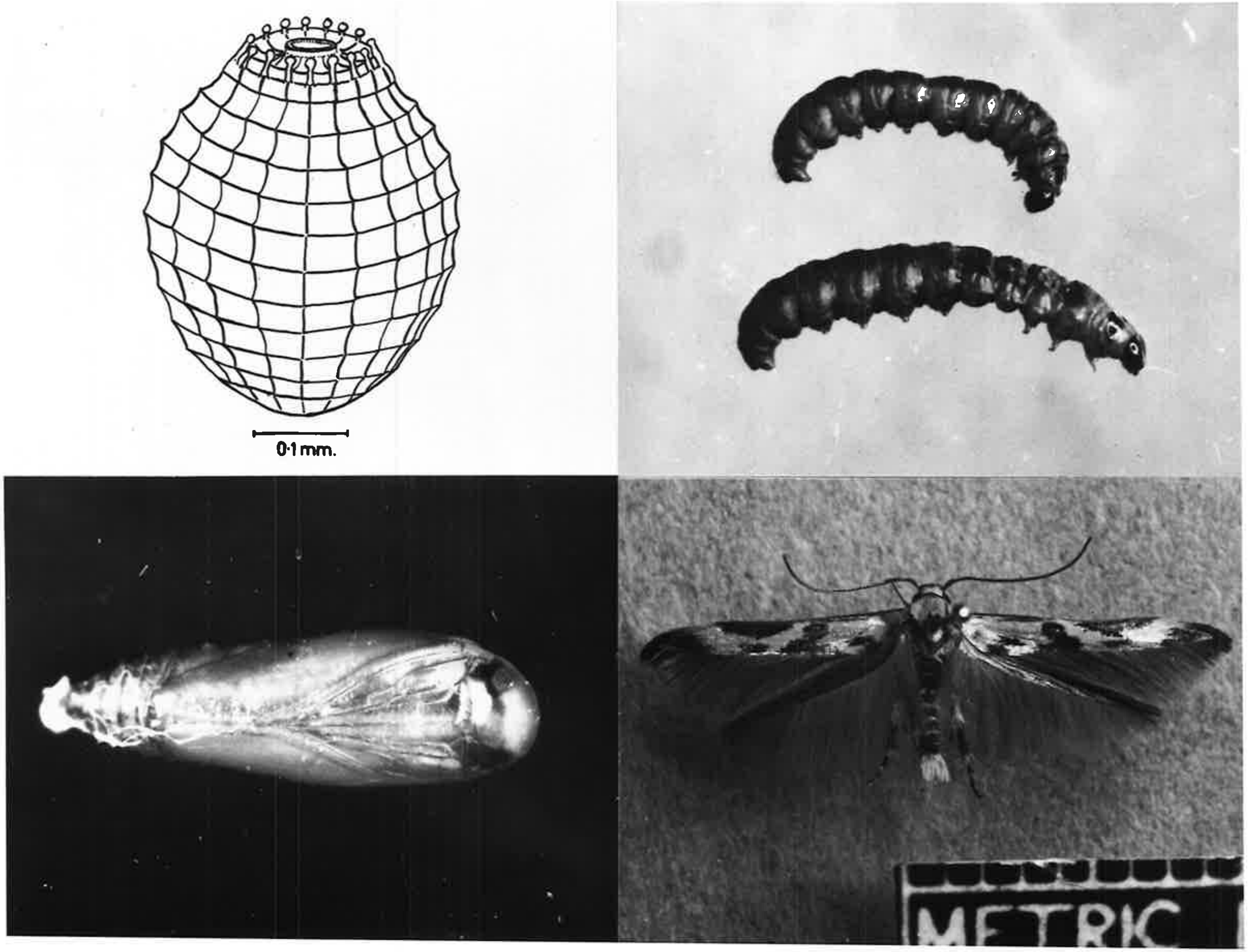
Stathmopoda melanochra

Egg

Mature larvae (x 10 approx.)

Pupa (x 20 approx.)

Adult


0·1 mm.
METRIC

substrate by the faecal matter evacuated from the gut before pupation. Larvae pupate beneath the tests of the scale they have destroyed (Figure 5.2). Some larvae fall from the tree and pupate in the ground.

Larvae of *P. beneficia* were commonly parasitized by *Quaylea* sp. (Encyrtidae) the adult wasp emerging from the pupa of the fly. The genus *Quaylea* contains at least one well known hyperparasite of hymenoptera (5.6).

P. beneficia occurred throughout the year but was not a parasite of major importance during the study. In January 1972 between 11.7 and 23.8% of scale on the trees near Alverstoke Orchard were killed by this species but in most samplings it killed less than 10% of the scale.

The adults (Figure 5.6) were frequently seen on ant-attended colonies where they easily avoided the ants and seemed to suffer little inconvenience. Ant attendance caused an increase in the number of scale killed by *P. beneficia* in November 1972 presumably because competition from *R. ventralis* was lessened.

5.5 Lepidoptera

5.5A Stathmopodidae: *Stathmopoda melanochra* Meyr

The genus *Stathmopoda* contains some 60 species in Australia. The larvae of most are herbivorous feeders on flowers; some tunnel in rust galls on *Acacia* sp. Two species are predatory, *S. melanochra* and *S. arachnophthora* Turn., the latter feeding in spiders' egg sacs (Common, 1970).

The egg, Figure 5.7, is laid in a crevice between adjoining female scale. As only the top half of the egg is usually visible it appears hemispherical in form and highly ornamented. When the scale are parted the whole egg becomes visible. It is ellipsoidal (almost round), .32 mm in diameter and .44 mm high and is laid in an upright position. The micropyle is surrounded by a circular ridge which is in turn surrounded by a coronet comprised of about fifteen cuticular projections. These extend down the outside of the eggshell as vertical ribs and are complemented by a series of horizontal ribs to form a reticulated network. The raised circular ridge at the apex of the egg is connected by radiating ribs to the cuticular processes of the coronet. When newly laid the egg is pink against which the raised white processes stand out under bright light. As the embryo develops the egg gradually turns paler in colour.

The first instar larvae begin spinning a silken tunnel between contiguous scale or under the overhang of a large female scale. The first instar larva does not seem to be predatory but feeds on the test of the female scale. Small larvae were frequently found in the test of dead female scale, the caudal opening of the scale being completely sealed up with silken web. As the larva grows it moves from scale to scale mining each scale and spinning a long silken tunnel between (Figure 5.2). Pieces of scale, faecal material and cast exuviae are incorporated into the roof of the tunnel. In this way up to 30 scale may be mined by one larva.

There appear to be four larval instars. The larvae increase in size from about 2 mm long when a couple of days old to a maximum of 7 mm before pupation (Figure 5.7).

The larval period lasted about 20 days at temperatures between 20 and 25°C. During this time larvae consumed 17-22 scale. The larval period may be greatly prolonged if the larva consumes all the available scale and may last at least six weeks, the larva feeding and pupating when given fresh scale. _S. melanochra_ is a true predator which mines living scale. It is also a scavenger in that colonies of dead scale are sometimes mined, but larger larvae require living scale before they can complete development. The larvae also gouge out and apparently feed on the bark of the tree under the tunnel, but this behaviour seems to be only of secondary importance. The larvae mine the adult female scale much more commonly than the nymphal stages of the scale.

The larva spins a coccoon in the tunnel where it pupates. The pupa (Figure 5.7) is light brown in colour, 4.3 mm long and 1.4 mm wide. The pupal period at 20-25°C is about 22 days.

Adults (Figure 5.7) were noticed at dusk in October 1972 flying around a tree with a large scale population. They were prevented from landing on the scale by the great number of ants (_Iridomyrmex_ sp. B) attending the scale. However in November 1972 the attendance of ants had no influence on the percentage of scale mined by larvae, which are concealed from the attention of the ants (4.3C).

The larvae are able to move very rapidly backwards or forwards in their tunnels but are highly adapted to this mode of life and once removed from the tunnels have great difficulty in forming a new mine. They obviously must rely heavily on scale being close together so that it is an easy matter to construct a tunnel from one scale to another. Larvae were rarely found in small colonies of scale where the density of the female scale was often sparse (5.8).

Larvae were found throughout the year and there appeared to be no marked seasonal periods of activity. S. melanochra was most effective in November 1972 on tree 1842A (Mallee Block) when 81.1% of the scale were mined. Some of these had probably been killed by R. ventralis before they were mined. The attack by S. melanochra was often sporadic. Despite the fact that scale on trees Obs. 1 and Obs. 2 in November 1972 were suitable for mining the percentage mortality on these populations was very low (4.0% and 0%) compared to the massive mortality on 1842A. An examination of Table 12 shows that this very high variability is not uncommon.

The larvae are parasitized by a species of Apantales. Extensive collections of the larvae were not made but of 18 collected in August 1973, 12 were parasitized.

Larvae of S. melanochra also mine Ceroplastes and Gascardia (Coccidae) near Sydney (Sands, pers. comm. 1969). The first instar larva of a stathmopodid was found in the ovisac of Pulvinaria ? dodoneae (Coccidae) collected at Loxton, South Australia.

5.5B Noctuidae: Catoblemma dubia (Butl.)
Catoblemma mesotaenia Turn.

C. dubia and C. mesotaenia are very similar. Patel, in 1969, bred out adults of C. mesotaenia from larvae feeding on E. coriaceus (specimens in the collection of the Department of Entomology, Waite Agricultural Research Institute). As the moths I reared from predatory larvae were

Figure 5.8

Catoblemma sp.

Egg (x 3 approx.)

Larva removed from its case (x 3 approx.)

Pupa of *C. dubia*

Adult of *C. dubia*


METRIC 1
METRIC 1

very similar to his I assumed they were the same species, however they were later found to be chiefly C. dubia (Common, pers. comm.). The following comments refer probably to C. dubia but because of the uncertainty I simply use "Catoblemma". The habits of C. mesotaenia and C. dubia appear to be very close.

The larvae eat all stages of E. coriaceus, and were seen feeding during the day and also at night.

The egg of Catoblemma sp. is round (.42 mm in diameter) and somewhat compressed (being .25 mm high). See Figure 5.8. The egg is laid in an upright position on the surface of the female scale or on the bark near the scale. Eggs are laid singly. Structurally the egg is much simpler than that of S. melanochra, being less ornamented and more compressed. The dorsal surface of the egg has a shallow depression with a central, slightly raised, micropylar area. The entire surface is covered by a reticulated network of ridges enclosing small cells which are somewhat irregular, being 4 or 5 sided. The egg shell of S. melanochra is half destroyed by the emerging larva whereas the larva of Catoblemma eats only a small hole in the side of the egg.

The larvae are easily recognized as they carry a case constructed from silk in which pieces of scale have been incorporated. The cases can be easily seen on twigs infested with scale in summer and may be up to 15 mm long. The enclosed larva, which is white with a black head capsule (Figure 5.8) uses the anal prolegs to clasp the case. The larva is able to move quickly on the twigs and yet hold the case firmly against the twig with surprising force when disturbed. The crochets on the prolegs are well developed and no doubt help in getting purchase on the twig. The larva feeds on the female scale by moving its case up until the front of the case touches the scale. The larva then protrudes its head from beneath the case and eats out the body of the female scale through a hole it makes in the test. Thus even when feeding, the body of the lepidopterous larva is not exposed for its case is closely pressed to the test of the scale and its head is hidden inside the test. The larvae are able to move over and feed on scale which are swarming with ants (*Iridomyrmex* sp. B) and seem to suffer little inconvenience. Occasionally cases were seen which had been torn open, presumably by ants, but this was uncommon. The larvae are parasitized by a braconid wasp (*Apantales* sp.).

Pupation occurs on the twigs or under the bark of the tree. Before pupation the larval case is firmly cemented to the twig; the walls are strengthened by further secretion of silk making the case extremely tough and the larva pupates inside it.

Larvae appeared in mid to late November and were seen on the survey trees until early April. There is probably an overwintering diapause as larvae were not seen from May to October despite the fact that scale were common during this time. As I have already mentioned (3.3D) *Catoblemma* was rare during the summer of 1971 - 1972 when there were very few larvae on only two of the survey populations. At this time, however, larvae were seen on *E. coriaceus* in the Adelaide Hills. In November 1972 - March 1973 larvae were found on most of the scale populations under observation.

When the larvae of *Catoblemma* were reared on female scale in the laboratory they usually removed the entire body of the coccid from the test, leaving the test with a gaping ragged hole. When the larvae fed on immature or small female scale it was not uncommon for the entire test of the scale to be removed, leaving only the base attached to the twig. The damage caused by *Catoblemma* larvae may be distinguished from that caused by *R. ventralis*. The two predators occur at different times of the year; scale devoured by *R. ventralis* are usually heavily stained by the red excrement of the larvae (Figure 5.2) whereas scale eaten by *Catoblemma* are more cleanly destroyed. Small coccinellid larvae are usually found in the scale when colonies from the field are dissected from August to November. The marks on the test caused by *Catoblemma* are obviously different from those of *Chrysopa ramburi* or *Stathmopoda melanochra*.

When a scale is attacked by hymenoptera the mummified body of the coccid, bearing the emergence holes, is usually left in the test. Occasionally in summer the top of the scale breaks away, or is taken away by ants, and the body of the coccid is also removed. Ants may also remove the bodies of scale killed by other means and the tests of such scale are very similar to those which have been attacked by *Catoblemma*. This was not realized at the beginning of summer in 1972 as *Catoblemma* had previously been quite rare. It was thus difficult to determine exactly what proportion of the scale in the field was destroyed by *Catoblemma*. The only method of assessing the impact of these predators, where there is some doubt on the extent of the damage they caused, is to examine the percentage mortality that can not be accounted for by any of the known predators or parasites.

Larvae attacked three of the six populations near Alverstoke Orchard and all three populations under observation in the Mallee Block. Table 5.6 shows the number of larvae (or pupal cases) of Catoblemma found on the trees and the proportion and number of scale whose cause of death was uncertain and which might have been killed by Catoblemma.

TABLE 5.6 The number of female E. coriaceus killed by unidentified causes and the number of moth larvae on those trees.

Tree	% female scale killed by unidentified causes	Total population of female scale	No. female scale killed by unidentified causes	No. Catoblemma larvae or pupae
A6	22.1%	10,892	2,407	18
A10	24.7%	221	55	3
A12	45.6%	423	193	8
1842A	43.1%	130	56	2*
1954B	68.8%	230	158	3*
1908B	16.0%	394	63	3*

* pupal cases

In late November and early December 1972, four larvae of Catoblemma were seen feeding on the large areas of young scale produced on tree A6 of the ant experiment; several coccinellid larvae were also present in late November. On 27th November when most of the young had been produced, it was estimated that 34,000 crawlers had settled; aproximately 24,000 of these would be females. About half of these settled as adult female scale in late December to produce the sizeable population of 10,900 females, survivors of which reproduced in January. It can be seen both from the small number of Catoblemma larvae present and the high survival rate of the immature scale that the predatory larvae could not prevent an almost ten fold growth in the number of female scale between November and December 1972.

By mid-January 1973, however, the number of Catoblemma larvae on this tree increased to 18 so that when the scale reproduced in mid-January a large number of Catoblemma larvae began to feed on the colonies of nymphs. When the adult female scale (i.e. in the population of 10,900) on this tree were sampled 77.1% of those examined could be accounted for as either alive, or killed by some known predator, or had died from an unknown cause which could not be Catoblemma. A large proportion of the scale (44.7%) was killed by hymenoptera. Thus 22.9%, or about 2,400 scale died from unidentified causes (superficially) resembling predation by Catoblemma. They could not all have been killed by the larvae of Catoblemma and many must therefore have been killed by another predator, or died naturally and had part of their test removed by the attendant ants. It seems unlikely that predation by Catoblemma, on this particular population of female scale, could have exceeded 5%. It can be seen that hymenoptera were the natural enemies which killed most female scale in this population and that the larvae of Catoblemma were relatively unimportant. When the female scale reproduced in January the moth larvae immediately began to feed on the colonies of crawlers as they formed. By

28th January only one colony of nymphs survived on a twig. When the colony was examined there were no surviving nymphs. Judging by the second instar tests on the twig about 74% of the nymphs had died and fallen off or were removed from the twig and all those remaining (26%) had been parasitized. The rate of parasitism was probably much higher as I found that mummified nymphs frequently fell off the twigs. The population was extinguished before March 1973 but the exact cause of the ultimate extinction could not be determined.

From such crude figures it is impossible to judge the relative importance of hymenoptera and *Catoblemma* as natural enemies on the population on tree A6. Sufficient to say that, acting together, they caused the extinction of a population in 1972 - 1973 very similar to that on Obs. 1 in 1971 - 1972 which increased from November 1971 to January 1972 and then doubled from January to March 1972 to a total of over 40,000 female scale.

An examination of Table 5.6 shows that on the other five trees many of the scale which had damage similar to that caused by *Catoblemma* were in fact probably killed by *Catoblemma* as each larva could consume about 10-20 mature scale of the size found in January. When the three trees from the Mallee Block were examined most of the scale had already been destroyed and only pupal cases of the moths remained; the number of larvae would have been greater than this.

In February 1973 the only population under surveillance still suffering attack by *Catoblemma* was that on tree A12 (near Alverstoke) where the predatory larvae were feeding on the nymphs of the scale.

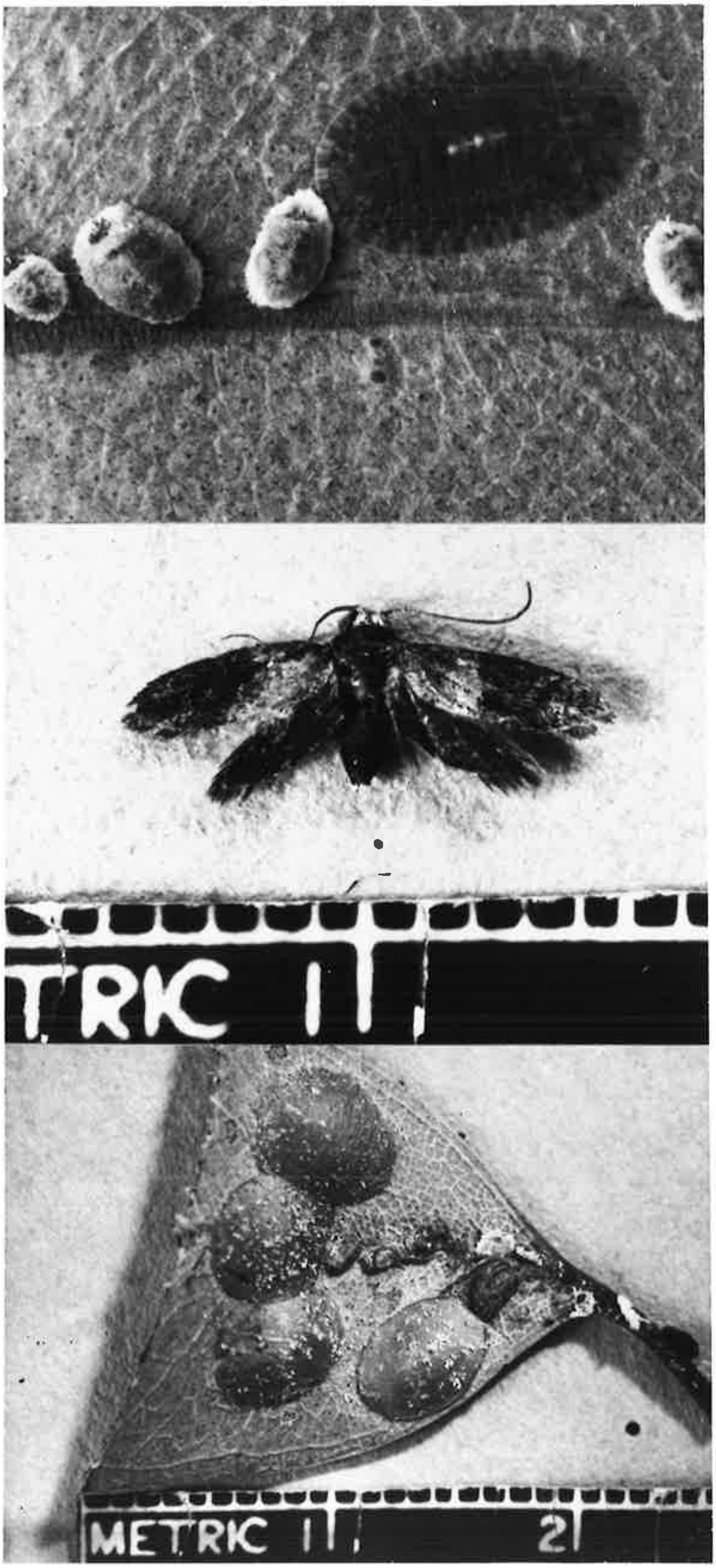
<u>Figure 5.9</u>

<u>*Cyclotorna*</u> sp.

Larva (note chiton-like appearance) (x 10 approx.)

Adult

Coccoons, one with a pupal case protruding.


TRIC 1
METRIC 1 2

Despite their presence more than double the number of female scale settled in late February than in the previous generation (1200 compared with 420) and by the time the females began to settle all the predatory larvae had pupated (thus the absence of any scale killed by *Catoblemma* in the population on tree A12 in March 1973).

Catoblemma was influential, with the hymenoptera, in causing the collapse of the population on tree A6. The populations on trees A10 and A12 survived and increased from January to March despite the presence of predatory larvae. The populations in the arboretum were kept at a low level partly through the influence of *Catoblemma*. Surviving scale were found deep in the umbels of fruit on 1842A and 1908B whereas in nearly all exposed colonies only the bases of the female scale remained, frequently with pupal cases of the moth nearby. In the previous year populations in the Mallee Block between January and April were generally higher and I believe this may have been largely because of the absence of *Catoblemma*.

5.5C *Cyclotornidae: Cyclotorna sp. near egena Meyrick*

The larvae (Figure 5.9) are highly specialized and are shaped very much like chitons (Amphineura, Mollusca). They have an articulated dorsal carapace of 11 plates, which is surrounded by a girdle of cuticular processes and these are tightly pressed to the surface over which the larva walks. When the larva feeds its head protrudes beyond the girdle but all appendages are hidden when the larva is resting. Ants had great difficulty in attacking larvae because the girdle was tightly pressed against the leaf and the ants could not grip the larvae with their mandibles. The larvae are approximately 4-5 mm long, 2.5 mm wide and .7 mm high.

The larvae feed on all stages of *E. coriaceus* and were collected at the Waite Institute in May and June 1973. They are not common and this species is not an important predator of the scale. Larvae pupate beneath the bark of the tree; the coccoon is almost flat and composed of tough silk (Figure 5.9). The adult is small, about 9 mm wing span (Figure 5.9).

Meyrick, in a supplement to a paper by Dodd (1911), described *C. egena* from moths reared by Dodd. Dodd describes the biology of *C. monountra*, the early larval stages of which feed on jassid leaf hoppers and the later stages on the larvae of the attendant ants. He found *C. egena* larvae in association with psyllids at Townsville, Queensland, and considered that they were feeding on the exudations of the psyllids. The paper illustrates the larval and pupal stages which are very similar to those shown here.

5.6 Hymenoptera

Scale killed by hymenoptera were easily recognized as they assumed a "mummified" appearance and the exit holes were obvious. The larval stages of the parasites were found when the living scale were dissected. The trends in the percentage of scale that were parasitized showed a marked increase in January and March, the times of sampling in summer and early autumn.

TABLE 5.7 Hymenoptera bred from *E. coriaceus* in January and March 1973.

January 1973

	Total	Percent	Mass rearings	1 per scale	2 per scale	Others
Aphycopsis sp. B	19	15.2	6	4	4	5
Aphycopsis sp. A	8	6.4	2	2	4	0
Myiocnema sp.	62	49.6	39	12	4	7
Cheiloneurus sp.	9	7.2	5	4	0	0
Quaylea sp.	12	9.6	3	3	4	2
Unidentified	15	12.0				
	125					

Mixed rearings

January 1973
2 x (*Myiocnema* sp. + *Aphycopsis* sp. B); (2 *Myiocnema* sp. + 2 *Aphycopsis* sp. B)
(2 *Myiocnema* sp. + 2 *Quaylea* sp.)
(*Myiocnema* sp. + *Aphycopsis* sp. B + Unidentified sp.)

March 1973
(*Myiocnema* sp. + *Aphycopsis* sp. A + Unidentified sp.)
(*Myiocnema* sp. + *Cheiloneurus* sp.)
(*Cheiloneurus* sp. + *Aphycopsis* sp. B)
(*Quaylea* sp. + *Aphycopsis* sp. B)

March 1973

	Total	Percent	Mass rearings	1 per scale	2 per scale	Others
Aphycopsis sp. B	39	22.8	25	4	8	2
Aphycopsis sp. A	17*	9.9	5	5	2	2
Myiocnema sp.	64	37.4	36	21	4	3
Cheiloneurus sp.	26	15.2	7	13	4	2
Quaylea sp.	7	4.1	1	5	0	1
Unidentified	18					
	171					

* Three *Aphycopsis* sp. A emerged from one female *E. coriaceus*.

In these months in 1973 two collections were made to determine the species composition of the hymenopterous fauna. Scale were removed from the bark and placed individually in gelatin capsules providing a collection of hymenoptera known to be primary parasites of the scale or hyperparasites. In addition sections of twig with parasitized scale were placed in lamp glass cages and the parasites collected. With this latter method parasites of the predators and Chamaemyiid fly parasites of the scale are also collected.

Hyperparasites destroy either the larvae, or the pupae of the primary parasite. Thus when scale which contained a primary parasite (which was hyperparasitized) are dissected one finds either the dried larval skin of primary parasite, with the meconium of the hyperparasite inside, or skeletal remains, especially the head capsule of the pupa of the primary parasite. When a primary parasite emerges from the scale only one sort of meconium is present and no skeletal remains are found in the ghost of the scale.

A list of the hymenoptera and their relative abundance is given in Table 5.7. The species named all come from _E. coriaceus_, (confirmed by rearings from isolated scale) and the table shows the results of isolated and mass rearings.

5.6A _Encyrtidae: Aphycopsis spp._

Two species of _Aphycopsis_ were bred from the scale and these appeared to be primary parasites. Dissections of scale from which they emerged revealed no pupal head capsules or other pupal remains. The scale from which these species emerged were frequently entirely eaten out, distended and translucent with the meconium of only one species inside. Two *Aphycopsis* emerged frequently from the one scale (and in one case three *Aphycopsis* emerged). These species were reared from scale with *Myiocnema* sp., *Cheiloneurus* sp., and *Quaylea* sp.

The genus Aphycopsis was erected by Timberlake (1916) from 2 females of a species (which he redescribed, *A. australiensis* (Howard)), which were bred from *Pseudococcus* sp., from Melbourne, Victoria.

The identifiable primary parasites constituted 21.6% of the total hymenoptera bred out in January and 32.7% in March 1973.

Aphycopsis spp. were capable of inflicting heavy mortality on both large and small populations. In January 1973 the following percentages parasitism and population sizes were recorded for the survey trees near Alverstoke Orchard: 37.9% (29); 79.2% (24); 44.7% (10,900); 71.4% (17); 49.5% (220); 38.0% (420). *Aphycopsis* spp. thus played an important part in the extinction of not only the smaller populations but also the largest population.

5.6B *Eriaporinae*: *Myiocnema sp.*

This species predominated in both rearings. The species bred from *E. coriaceus* seems very similar to *M. comperi* (Ashmead)(formerly *Euryischia comperi*) redescribed by Smith and Compere (1928). Dumbleton (1940) reared *M. comperi* from *E. coriaceus* collected at the Waite Institute and it seems likely that the species bred out in the present study is the same. Specimens have been sent for confirmation of this identification. *M.*

comperi was bred in U.S. from black scale (Saissetia oleae) collected in Sydney N.S.W. Smith and Compere (1928) were unable to determine the status of M. comperi but there is evidence that the species of Myiocnema bred from E. coriaceus is a hyperparasite. Scale from which only Myiocnema emerged invariably contained part of a head capsule and other pupal remains, undoubtedly all that was left of the primary parasite. Dumbleton (1940) also records it as a hyperparasite

Oneadult usually emerged from a scale. Adults of this species emerged with every other identified species of parasite but the significance of this is unknown.

5.6C Encyrtidae: Cheiloneurus sp.

Scale from which only Cheiloneurus sp. emerged contained head capsules or evidence that the scale had previously been inhabited by other hymenoptera, indicating that this species is a hyperparasite. Smith and Compere (1928) and Rosen (1969) have recorded species of Cheiloneurus as hyperparasites.

One adult usually emerged from a scale, seldom two, and the species was reared (from the one scale) with Myiocnema sp. and Aphycopsis sp. B.

5.6D Encyrtidae: Quaylea sp.

The genus Quaylea was erected by Timberlake (1919) for Q. whitteri (Gir.). Smith and Compere (1928) illustrate Q. whitteri, which is close in general appearance to the species bred from E. coriaceus, and discuss the history and synonomy of the species. Q. whitteri is a hyperparasite which has been bred from many species of (parasitized) scale (Smith and

Compere 1928, Timberlake 1919). Note that the species described by Timberlake in this paper (with a list of hosts) as *Q. aliena* is in fact *Q. whitteri*. (See Timberlake 1921).

Q. whitteri was introduced into California in the mistaken belief that it was a primary parasite. Initially Smith and Compere (1928) considered it did a great deal of damage to the biological control programme by suppressing the primary parasites of black scale but De Bach and Bartlett (in De Bach 1964) comment on the low efficiency of the primary parasites of black scale despite the fact that by this time *Q. whitteri* was a rarity.

A careful dissection of scale from which only *Quaylea* sp. had emerged showed the skin of the larva of the primary parasite inside which was the meconium of *Quaylea* indicating it was a hyperparasite. Smith and Compere (1928) found *Q. whitteri* the most common hymenopteran they from black scale collected in Sydney N.S.W. but in the present collections *Quaylea* sp. was less common.

One *Quaylea* usually emerged from one scale. *Quaylea* was found in association with *Myiocnema* and *Aphycopsis* sp. B.

5.6E Unidentified species

The unidentified specimens probably contain both primary parasites and hyperparasites. Because many of the keys to the Encyrtids require females it was not possible to place some of the males even in a genus (Cardale pers. comm. 1973). The number of unidentified specimens is not sufficient to alter the overall picture which is one of a high rate of hyper-parasitism, particularly by *Myiocnema* sp. This may be because the collections were made at the end of summer when the rate of hyperparasitism is likely to be high (Fisher in De Bach, 1964).

In addition to these species Dumbleton (1940) bred *Metaphycus* sp. from *E. coriaceus*. Patel (1971) reared *Aphycaspis ? eriococci* Timberlake (Encyrtinae) and *Euryischomiia* (Eriaporinae), the latter being a hyperparasite (Riek pers. comm. 1969).

There are probably changes in the seasonal composition of the hymenopteran fauna as well as many interesting interactions between the different species. Before the fauna can be investigated in detail it will be necessary to describe the species and to rear each species to determine the status of the males and the relationships of the hyperparasites.

5.7 Arachnida

5.7A Araneida

Spiders of two families, Salticidae and Theridiidae were collected from the small trees used in the experiment at Kuitpo Forest (Chapter 6) in late November 1973. There seemed little doubt that they were feeding on the young scale as there were no other prey on the trees at the time. Lines of spider web were frequently seen when colonies of scale were examined but it seems unlikely that spiders kill many scale.

5.7B Acarina

Two species of mites were found in association with *E. coriaceus*. Mites of the genus *Stenotarsonemus* (Tarsonemidae, Heterostigmata) are usually considered phytophagous while those of the genus *Tydeus* (Tyeidae, Promata) are usually regarded as predators (Lee 1973 pers. comm.).

The latter might well have been preying on the phytophagous mites although they were sometimes found under the tests of dead female scale. Whether they were the cause of death of the coccids or merely seeking refuge under the tests was not determined.

5.8 The influence of colony size on the survival of *E. coriaceus* and the extent and causes of mortality

If the data for the smaller colonies on each tree (both attended by ants and unattended) are paired against the data for the larger colonies on the same tree (Table 4.3) the influence of the size of the colony on survival of *E. coriaceus* and the extent and causes of mortality can be determined.

Survival in larger colonies was significantly higher than in small colonies. Mean percentage survival for scale in the 10 larger colonies was 24.7% and in the 10 smaller colonies 8.3% ($t = 6.77$; 9 d.f.; $p < .005$). On this basis I expected a regular relationship between colony size and survival but when all the census data was examined this was not so. On only 3 of the 10 trees were there significant correlations between ranks in colony size and survival. There is some possibility that survival might increase as colony size increases but the data are much too variable for any conclusions to be reached.

A greater percentage of scale in small colonies was killed by coccinellids than in large colonies (83.6% compared with 50.5%; $t = 4.780$; 9 d.f.; $p < .005$).

Larvae of *P. beneficia* killed more scale in large colonies than in small colonies (combined data for ant-attended and ant-free colonies, $t = 2.34$; 9 d.f.; $p < .05$). There was competition between the natural enemies for prey. This was particularly noticeable on tree A1 (which had a small scale population attended by ants) where scale already attacked by larvae of *P. beneficia* were destroyed by *R. ventralis*, causing the death of the fly larvae. In unattended populations the coccinellid killed many of the scale before *P. beneficia* could lay, or at least before the larvae could develop sufficiently so that the host scale became unattractive to *R. ventralis*. In attended populations predation by *R. ventralis* was reduced and the fly had less competition. Fly larvae probably survived better in large colonies because they could move more easily from scale to scale, as the density of female scale in larger colonies is often greater than in small colonies.

S. melanochra was found only in large colonies. This is to be expected because in the small colonies the female scale are frequently far apart and the larvae of the moth can not construct tunnels (over long distances) where there are no scale. Whether the female moth has any preference for laying eggs in dense colonies is unknown. Eggs and first instar larvae have been found on isolated scale, but are much more commonly found on dense colonies.

The percentage of scale killed by hymenoptera and to causes which could not be identified were the same in both small and large colonies.

CHAPTER 6

Intra-specific mechanisms and their importance in the ecology of *E. coriaceus*

In the course of the survey on the observational trees it was clear that, although populations of *E. coriaceus* were usually kept at low levels by the action of the many natural enemies or perhaps hot weather in summer, at times populations on individual trees became large enough to cover an appreciable proportion of the available surface area of the tree. When this occurred several density-induced negative feedback processes came into operation. At high population densities:

1. Many of the mobile stages, i.e. larvae and early adult females, emigrated from the tree.
2. The mean size of the females at reproduction decreased, and so did their fecundity.
3. The sex ratio of the young produced by these small females changed from predominantly female to predominantly male.
4. The densities of the females in the colonies increased and caused, in some instances, reduced fecundity because of physical crowding.

Evidence for these processes was also obtained from several simple experiments. This evidence is presented below. A more comprehensive experiment was performed on a large number of small trees and this is described in 6.2. The consequences and importance of the intra-specific mechanisms are then discussed.

6.1 Initial observations

6.1A Emigration of the mobile stages

The emigration of mobile scale from trees observed in November 1971 (Obs. 1 and Obs. 2) has been discussed (1.6F).

A similar but more pronounced emigration occurred on another tree nearby where over 95% of the crawlers left the tree and walked over parked cars and the fence nearby. On this tree there was initially a large population of female scale which suffered almost no mortality when they began to reproduce (probably because they were well attended by ants). So many larvae were produced that the leaves and twigs of the tree begin to die as the larvae started to settle and it appeared as if the whole tree would die. Large numbers of crawlers left the tree and eventually it seemed that all the larvae had gone. However, after some weeks an examination of the tree showed that it was slowly recovering and that a small population of female scale derived from some nymphs that had remained and developed, were surviving. These later reproduced.

6.1B The influence of population density on the size of the female scale at the time of reproduction

In November 1971 two similar adjacent trees had greatly differing scale populations. In November, Obs. 1 had a population of 14,900 females and Obs. 2 a much greater population of 30,200 females. At the time of reproduction the mean size of the female scale on the two trees was different, 3.17 ± .05 mm and 2.80 ± .05 mm respectively ($p < .001$). In the next generation (January 1972) the situation was reversed as the population on Obs. 1 increased from 14,900 to 21,700 and that on the second tree decreased from 30,200 to 1,900; the scale on Obs. 2 were significantly larger than those on Obs. 1, the lengths being 2.20 ± .09 mm and 1.87 ± .04 mm respectively ($p < .05$).

From August to November 1972 an attempt was made to induce high populations of scale on two trees in a large field cage; two other trees in the cage were to have low populations for contrast. However, predators entered the cage through a breach made by a storm and destroyed many of the scale so that a large population could be produced on only one tree. The properties of the females in this population, which contained over 50,000 scale and covered over 80% of the surface area of the tree, were compared with those on the two populations where the numbers of adult female scale were below 1,000 and covered negligible proportions of the trees.

When reproduction began the mean length of the females on the three trees was measured. For reasons which will be discussed later only scale which did not touch their neighbours were measured from the tree with the highest scale population. The colonies of females on the trees with low populations occurred where twigs were .3 to .5 cm in diameter (the preferred settling sites). On the tree with the high scale population, twigs and branches of all diameters were colonized. As there appeared to be a difference in size between the females at the tips of the twigs and those situated proximally, both areas were sampled. The scale from the tips were significantly larger than those at the usually preferred site (2.55 ± .06 mm and 2.05 ± .06 mm respectively, $p < .001$). The significance of this finding is discussed later. Scale from both areas were significantly smaller than scale from the two trees with low populations ($p < .001$). The sizes of the female scale in the two low populations were similar ($3.12 \pm .05$ mm and $3.01 \pm .03$ mm).

There is thus a reduction in female size (and hence fecundity) as the population density increases.

6.1C The influence of population density on the sex ratio of the young produced

The unusual method of sex determination in coccids (see 2.4) prompted me to examine the sex ratio of the young.

In November 1971 the sex ratio of the young produced on the two trees previously mentioned (Obs. 1 - 14,900 females and Obs. 2 - 30,200 females) was measured crudely by placing a potted tree, supported on a frame, in the foliage of each of the trees when the females were reproducing. Crawlers walked onto these smaller trees which were removed after several days and kept until the sex of the larvae could readily be determined. The young collected from Obs. 1 were predominantly female (981 ♀♀ and 561 ♂♂; 63.6% females) but those from Obs. 2 were mainly males (288 ♀♀ and 836 ♂♂; 25.6% females).

The sex ratios of the young produced by the females on the three caged trees described above were also examined. Sections of twigs bearing pre-reproductive females were removed (8 from the crowded tree and 4 from each of the uncrowded trees) and tied onto potted trees. Female nymphs predominated in the young from both trees with low populations.

From the samples from one tree 1991 nymphs developed and the mean sex ratio was 72.8% females (range 63.6% to 91.6%); from the samples from the other tree 1830 nymphs developed and the mean sex ratio was 70.2% females (range 69.2% to 71.6%). From the tree with a large scale population 1212 young developed and the mean sex ratio was 23.0% females (range 5.8% to 46.4%).

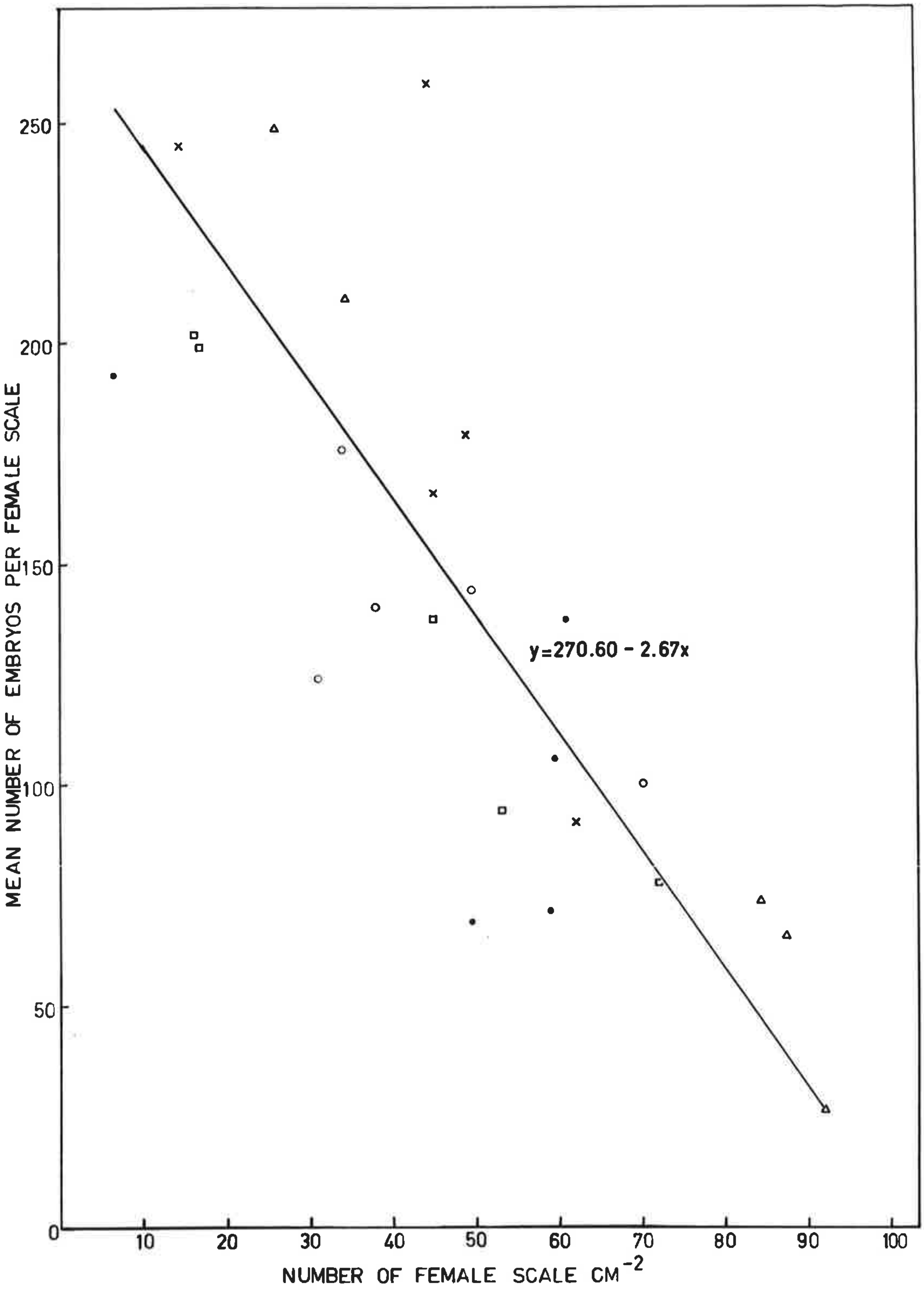
6.1D The influence of colony density on the fecundity of the females

There was no overall correlation between the number of scale on a tree and the mean density of the colonies, however on one tree (Obs. 1) colonies of extremely high density (up to 100 scale per cm^2) were formed in January and March 1972 when the numbers of female scale on the tree were very large (21,600 and 41,500 respectively). An appreciable percentage of the total surface area of this tree was, or had been occupied by female scale (see 2.2B) and I believe the formation of very dense colonies of females was a result of crowding. These were the densest colonies seen in the study and occurred on the only tree with a very large population of females maintained through several successive generations.

In January 1972 conditions on this tree were ideal to examine the influence of colony density on fecundity in a field population. Percentage survival of the females when most were about to reproduce was relatively high (48.5%) and this was important because if mortality is high the few surviving females can expand, crush the tests of their dead neighbours and grow to a larger size (and be more fecund) than anticipated on the basis of density measurements alone. In the dense colonies it was

Figure 6.1

The influence of colony density on the number of embryos contained by female *E. coriaceus*. Samples were taken from five branches; the same symbol is used for the data from each branch.


MEAN NUMBER OF EMBRYOS PER FEMALE SCALE
0
50
100
150
200
250
10
20
30
40
50
60
70
80
90
100
NUMBER OF FEMALE SCALE CM^{-2}
y=270.60 - 2.67x

impossible to measure the length of the females accurately for their tests had been secreted so that, in places, they formed a continuous mat. The bodies of some females extended far beyond the area delineated by the visible area of the test and the bodies of others (which, from an examination of the top of the test appeared normal) were greatly constricted. Scale were therefore dissected and the number of embryos counted. The number of embryos a scale contains just before reproduction is closely related to the number of young she can produce (see 2.3A).

Observations to examine the relationship between density and the number of embryos were performed in the following way. Five branches which had colonies of greatly differing densities were chosen from the tree. From each of these branches five samples, bark slivers or sections of twig, were removed to cover as wide a range of densities as possible. Each sample was stored at 5°C until it could be dissected. A subsample of five females was then chosen at random from the survivors in each sample.

The density of the scale was estimated by using a pair of vernier calipers (if a section of twig was removed) or by tracing the bark sliver onto mm graph paper with a sharp pencil and estimating the area covered.

Figure 6.1 shows the data for the five branches. On each branch, the mean number of embryos decreased as the density increased, the regression for the pooled data being highly significant ($F_{1,23} = 216.9$; $p < .005$).

Smirnov and Polejaeff (1934) demonstrated that the mean fecundity in Lepidosaphes ulmi, (Homoptera:Diaspididae), decreased as the density of the females in the colonies increased. They found that the decrease in the mean number of eggs per female was not caused by a general reduction in fecundity but rather that the proportion of sterile females increased with increasing density. Indeed at high densities fertile females produced as many eggs as at low densities. This is not so for _E. coriaceus_, where there was a general decrease in fecundity and no increase in sterility. A total of 94 scale were dissected from colonies with a density above 60 females per square cm and 158 from colonies of lesser density. There were 2 and 0 scale respectively with no ovarian development. Examination of small crowded females from other colonies of extremely high density showed that many were producing young.

The consequences of such crowding can be estimated. At low densities (20 females per square centimeter) about 4,340 young are produced per square centimeter of infested tree area, whereas at high densities (90 females per square centimeter) about 1,710 crawlers are produced per square centimeter of infested tree area.

6.2 The experimental examination of certain consequences of crowding

So far intra-specific mechanisms have been examined as they operated on populations of scale on trees 2-3 m high. The size of the tree was obviously an important factor in determining whether negative feedback mechanisms came into operation, for on a tree 2-3 m high at least two consecutive generations, completed under conditions highly favourable for the survival of the scale, were usually necessary before the population of the scale became large enough to cause noticeable crowding.

The chance of predators or weather reducing the population during this time was very high. On only four occasions during the survey from August 1971 to March 1973 did larger trees have populations where severe overcrowding occurred.

E. coriaceus commonly occurs in the wild on small seedlings and trees, particularly *E. camaldulensis*, .5-1 m high. On such trees where the offspring from a few females would saturate the surface area of the tree, overcrowding and the attendant density-dependent effects must occur commonly. In a survey in September 1973 in the Kuitpo Forest Reserve 7 of the 28 infested trees examined were small and had populations of females sufficient so that their offspring would cover a large proportion of the surface area of the tree. Both the scale and the trees showed the effects of overcrowding. The female scale were smaller on trees where they were more numerous. These trees also showed obvious signs of stress, losing many leaves and having a stunted appearance.

It was impossible to study the consequences of overcrowding in natural populations. In the study area at the Waite Institute overcrowding rarely occurred and in wild populations, where it was more common, infested trees were usually very far apart and often growing under different conditions. Therefore I decided to examine overcrowding experimentally.

6.2A Methods

I wished to investigate the relationship between the population density of nymphs and the number of adult females that settled on the tree. The influence of population density on the size of the females at reproduction, the sex ratio of the young they produced and the rate of growth of the tree were also examined.

The most convenient way of determining the influence of nymphal population density on the number remaining on the tree and settling as adult females was to seed early second instar (or late first instar) nymphs onto the tree. These settled and developed, eventually moulting to give the (mobile) early adult female stage. The females which settled on the tree could be readily counted. The number of female second instar nymphs which completed development and moulted was also easily estimated as they secrete a frail but lasting test which remains on the twig after the scale has moulted. The males feed for only 2-3 days before they pupate and are therefore of no consequence (in terms of competition).

The size of the resulting females at the time of reproduction was measured and the sex ratio of the young they produced was determined by removing twig sections containing reproducing females and allowing the nymphs to settle and develop on other trees.

I had difficulty in finding a large group of small gums of uniform size in an area where people would not interfere with the experiment. In South Australia seedling gums grow in some _Pinus radiata_ forests where they form part of the undergrowth. This is cleared periodically and thus stands of seedling or regrowth of _Eucalyptus_ trees of one species and uniform age can be obtained. A suitable area was found in Kuitpo Forest which lies about 50 km south of Adelaide in the Mount Lofty Ranges at an elevation of about 200-300 m. _E. obliqua_, about .75 m high and

Figure 6.2

Two (poor) photographs showing the experiment at Kuitpo Forest.

Upper photograph shows a small tree and the cage used.

Lower photograph shows some trees in Series I. (Some bigger caged trees are also shown. Twigs bearing female scale collected from several areas were tied onto these. The young the females produced mixed and these were later used to seed the experimental trees).

growing from small tubers, occurred along a firebreak (Figure 6.2) and in a very open patch of Pinus radiata. The trees had between 11 and 36 mature leaves and 6-84 immature leaves and primordia each and usually a single stem with one or two side branches. Forty small trees were chosen, for convenience, in two series of twenty trees each.

The lengths of the main stem and all side twigs in the first series (henceforth Series I) of trees were measured before the nymphs were seeded onto them. The twigs and stem were simply stretched on a centimeter rule and the total length for the tree measured to the nearest .5 cm. The leaves were also counted. These measurements were made primarily so that the influence of population density on tree growth could be measured but they also proved useful in interpreting other results. Unfortunately the stem and twig lengths of the trees in the second series (Series II) were not measured. Only the data from Series I trees can thus be corrected for tree size. Data from Series I are also used (with data from Series II) without corrections for tree size.

I expected that 200-400 female scale would be sufficient to saturate the trees. Ideally trees were to be seeded with a range of 5 to about 600 female second instar nymphs but as it was impossible to estimate the number seeded, the treatment densities were variable and covered a wide range. Both the stock of females (which gave the nymphs to be seeded onto the experimental trees) and the nymphs were randomized. Twigs bearing the females were tied onto large caged trees and the young they produced were allowed to develop until some began moulting to the second instar. Sections of twig bearing the nymphs were cut off and transferred to the experimental trees where the second instar nymphs settled. The twenty trees in the first series were seeded on 9th October and those in the second series on 15th

October. Very few nymphs settled during the first six days, most remaining on the twig sections. To try to achieve the desired densities in the second series I increased the numbers of nymphs seeded onto the trees. The poor initial rate of settling was almost certainly due to cold weather as most of the nymphs eventually left the twig sections and settled on the experimental trees. The trees in Series II thus had a higher number of female nymphs than those in Series I.

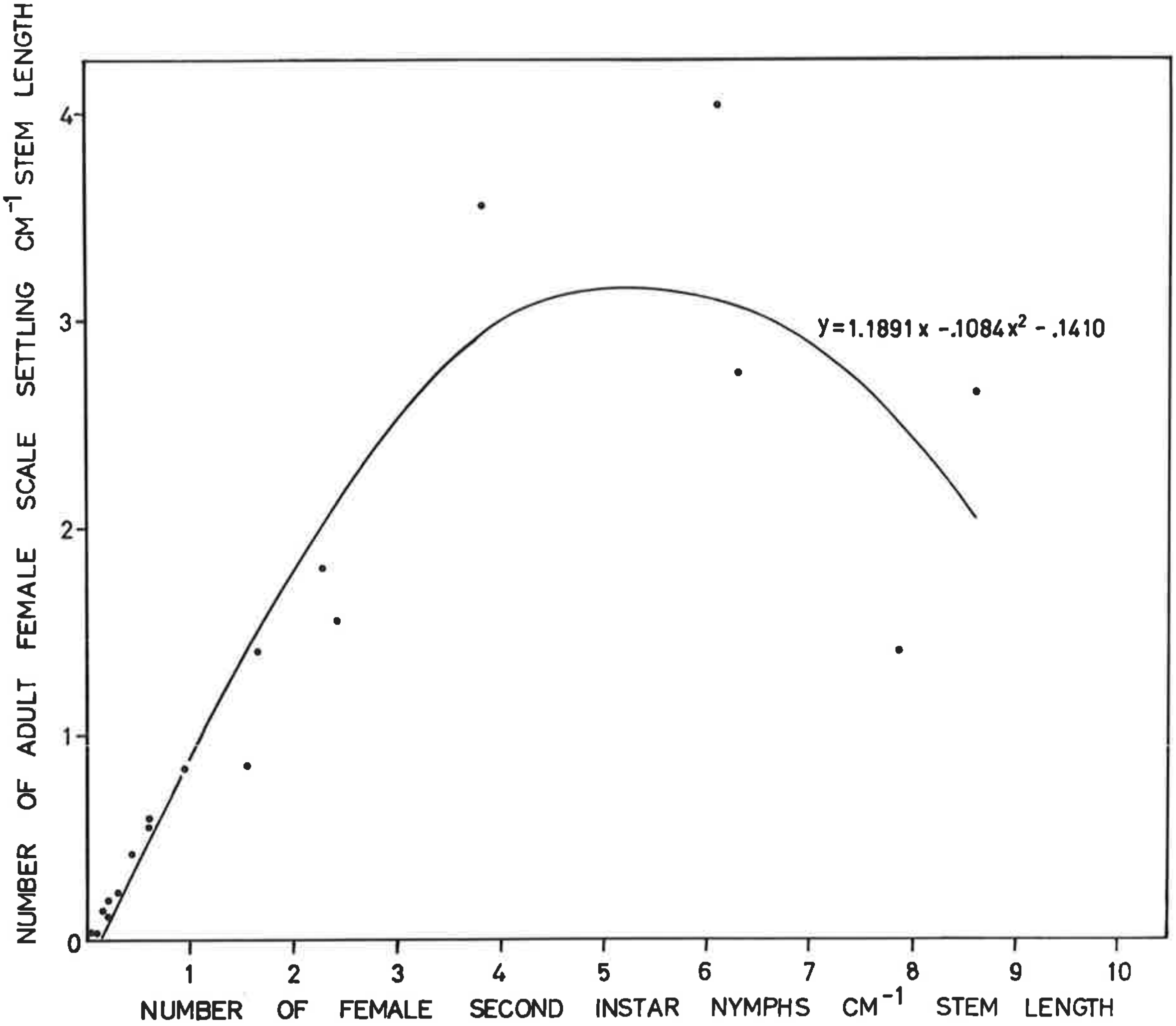
A cage was made for each tree (Figure 6.2) from butter muslin and cheesecloth (the latter was used to form a heavy skirt at the bottom of the cage making a seal with the ground).

By 22nd November all the second instar females had moulted and those adult females which were going to stay on the trees had secreted their tests. All trees were examined using a magnifying headpiece or a binocular microscope. The vacant tests of the female second instar nymphs (i.e. those second instar females which had survived and moulted) and the adult females which had secreted their test were counted.

I expected that 200-400 females would be the maximum number that would settled on the trees. Where there were fewer than 200 female second instar nymphs which moulted to the female stage all (or a large proportion) of these would settle on the tree and develop as females. As the number of larvae that moulted exceeded the carrying capacity of the tree the number of mobile newly moulted females leaving the tree would increase and the number remaining on the tree stabilize. Thus the plot of the number of females against the number of second instar females moulting would be curved with an asymptote above about 200 female second

Figure 6.3

The numbers of adult female E. *coriaceus* settling and secreting tests from varying numbers of female second instar nymphs. (Data corrected for the size of the tree).


NUMBER OF ADULT FEMALE SCALE SETTLING CM^{-1} STEM LENGTH
0
1
2
3
4
1
2
3
4
5
6
7
8
9
10
NUMBER OF FEMALE SECOND INSTAR NYMPHS CM^{-1} STEM LENGTH
$y = 1.1891x - .1084x^2 - .1410$

instar nymphs.

Of course this was not the only possible outcome. It was possible that an equal proportion of larvae would have settled at all densities indicating that walking off was a chance event and not related to the initial density at all.

6.2B Results

a. The influence of the initial numbers of second instar females on those remaining and settling as adult females

All values for both series of tree are tabulated (Table 15 Appendix). Analysis indicates that although the regression of the number of adult females settling and secreting their tests on the number of female second instar nymphs that moulted to the adult stage is linear the data does have a distinct element of curvature because the reduction in the sum of squares when the quadratic term is introduced is almost significant at .05 level.

The curvature is obscured by the settling rate on one tree, where 730 females of the initial 780 female second instars settled. This tree was the largest used in the experiment and was in Series I where tree size had been measured. A correction for the size of the tree can be made by dividing both numbers of second instar females and numbers of adult females settling on the trees in Series I by the stem length of the tree (Table 16 Appendix). These data deviate significantly from a linear regression ($F_{1,16} = 28.43$; $p < .005$) and are well fitted by a second degree polynomial ($F_{2,16} = 48.63$; $p < .005$). The points and fitted curve are shown in Figure 6.3.

The settling rates are therefore not random (which would have given a straight line relationship) but obviously a greater proportion of newly moulted females settle on the less crowded trees than on the more crowded. My assumption that an asymoptote would be formed may be wrong for in Figure 6.3 there is a decline in the numbers settling at very high densities.

Many mobile females walked off the trees. Grease traps on plastic sheets were placed around the bases of some trees and large numbers of scale were trapped. Walking off is thus an important phenomenon in the regulation of population density on these small trees.

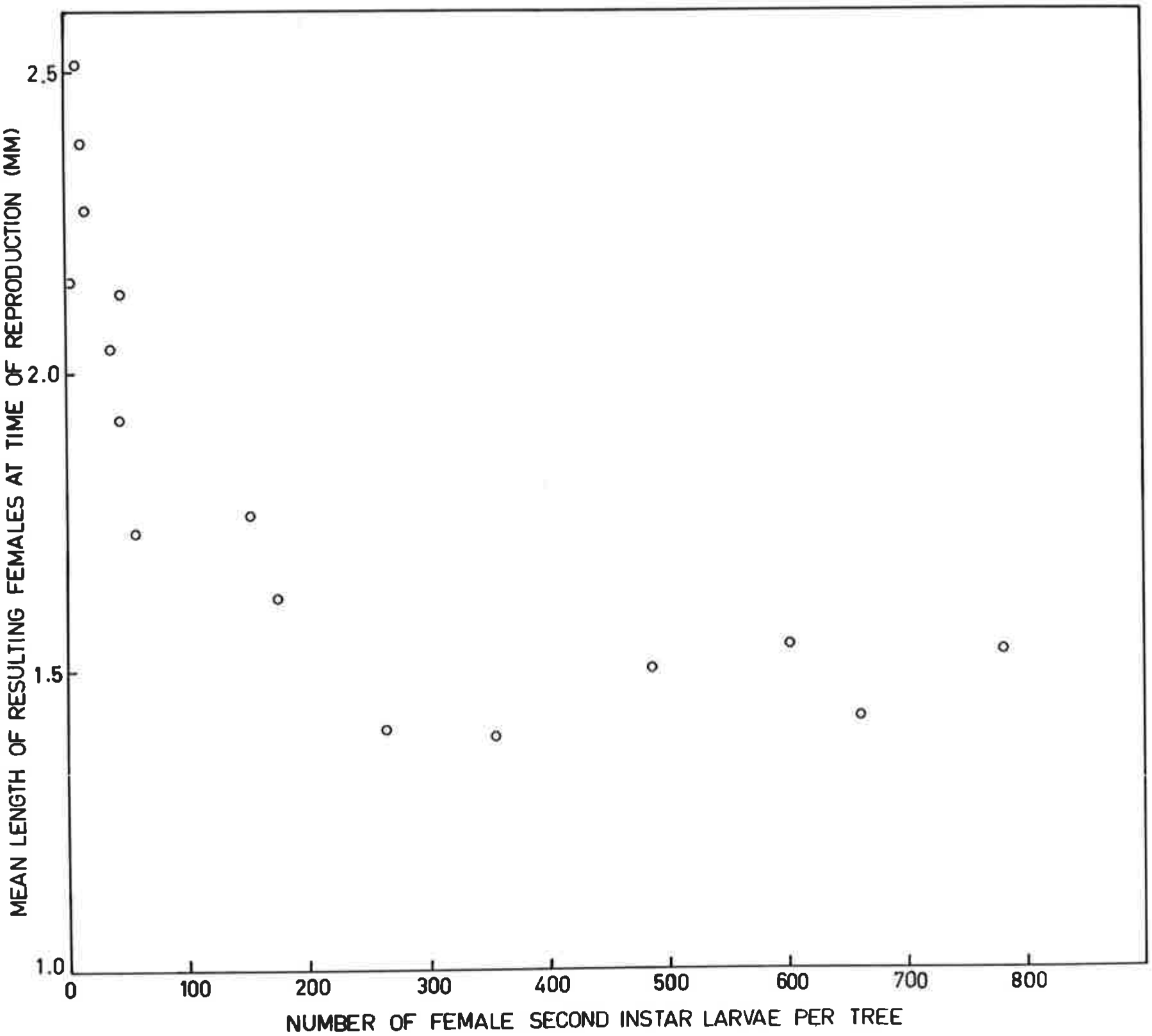
b. The influence of density of female second stage nymphs on mean length of adult females derived from them

The mean length of a sample of surviving females from each tree in Series I and Series II was determined between 17th and 22nd December when females on many of the treesbegan to reproduce. From some trees twig sections bearing female scale were removed, the sizes of the females measured and the sections tied onto uninfested caged trees so that the sex ratio of the young could be determined. On many trees the size of the scale was measured on the tree, which was bent over onto the stage of a binocular microscope supported on a stand. (I hoped to measure the number of crawlers produced and emigrating from these populations but this proved impossible).

The lengths of the females may depend on one (or all) of the interactions between scale, or between scale and tree in either the nymphal or adult stage of the scale. These interactions will initially be

Figure 6.4

The influence of number of female second instar nymphs per tree on the size of the resulting female scale. (Series I).



MEAN LENGTH OF RESULTING FEMALES AT TIME OF REPRODUCTION (MM)
2.5
2.0
1.5
1.0
0
100
200
300
400
500
600
700
800
NUMBER OF FEMALE SECOND INSTAR LARVAE PER TREE

Figure 6.5

The influence of number of female second instar nymphs per tree on the size of the resulting female scale. (Series II).

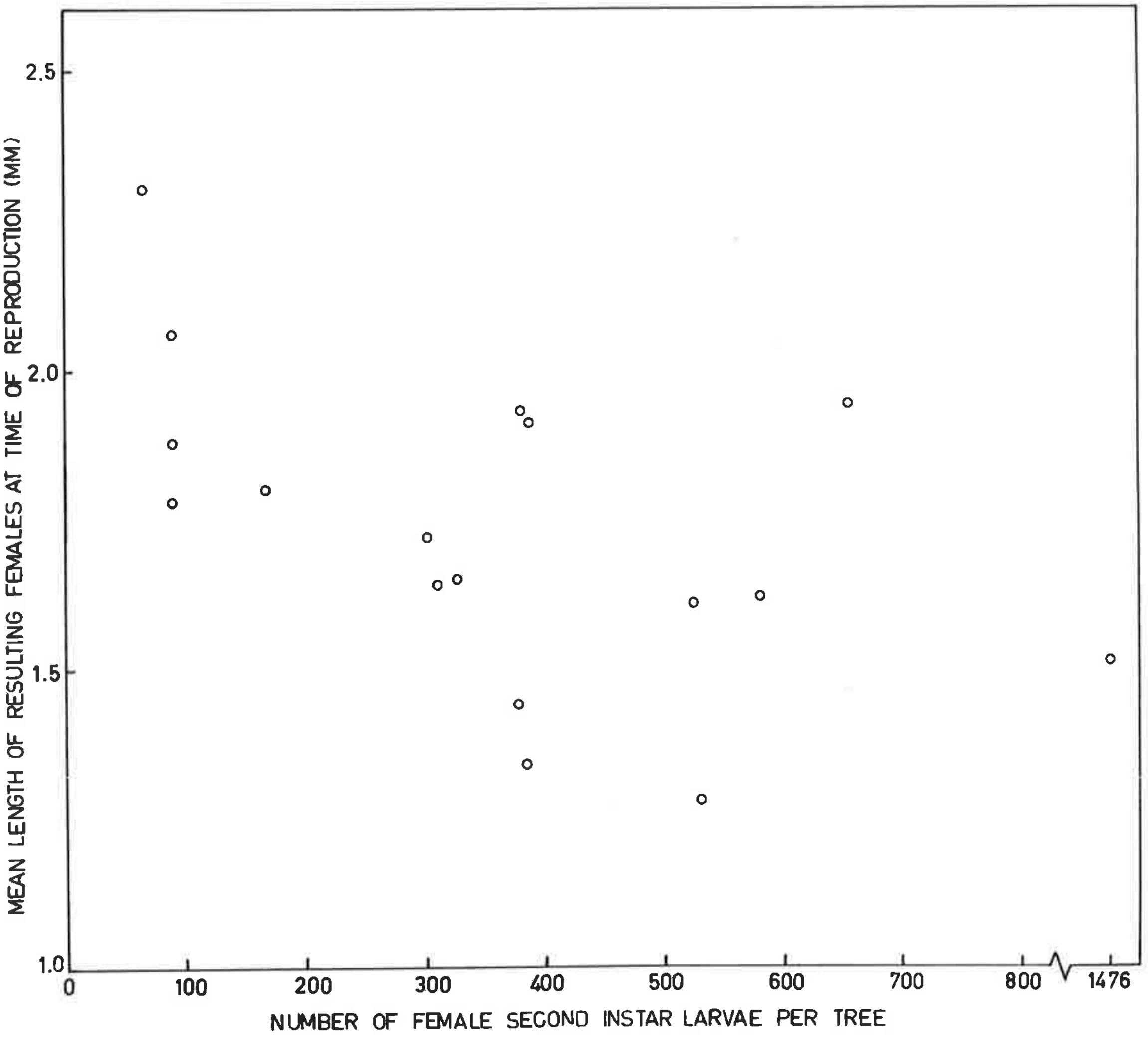
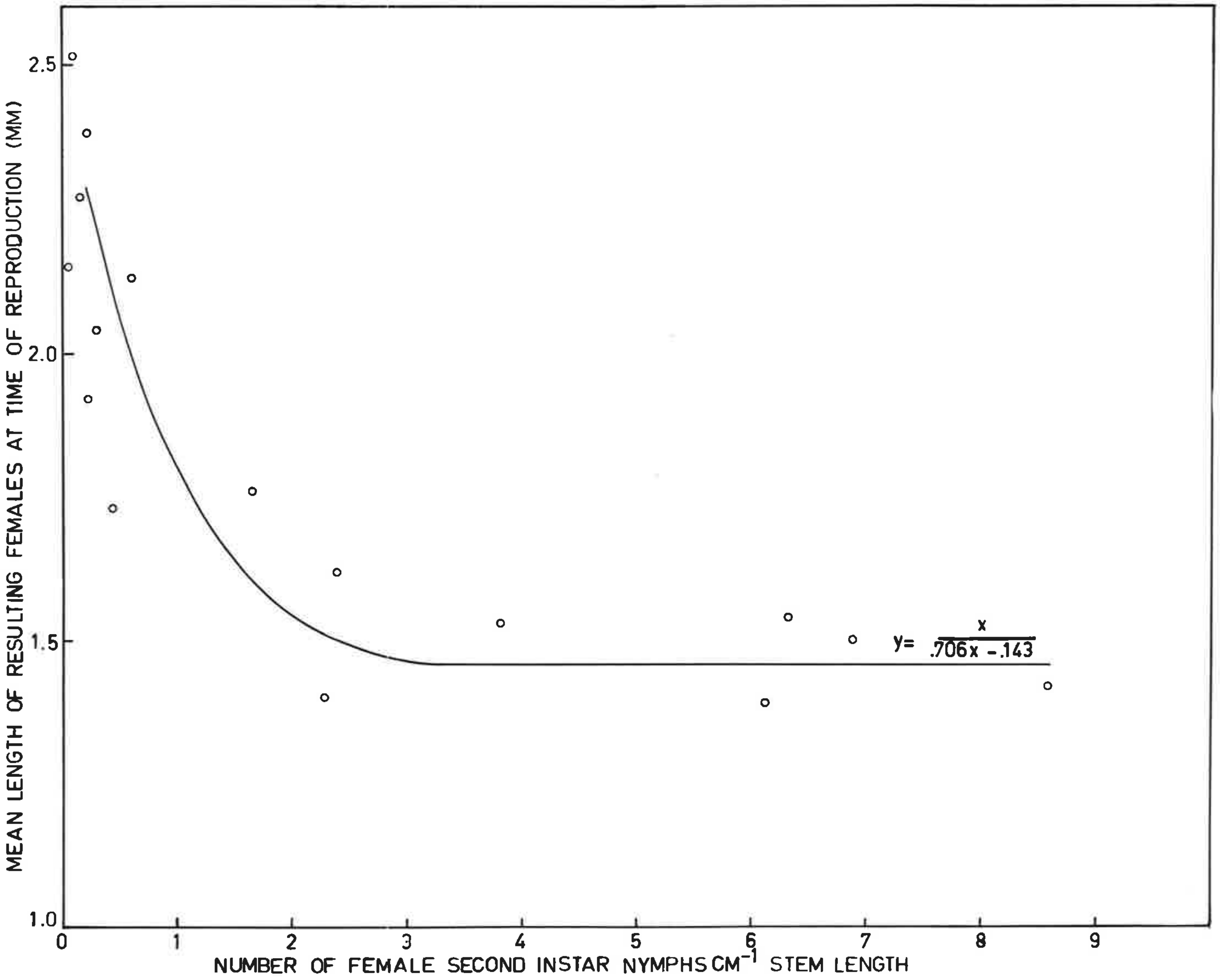

MEAN LENGTH OF RESULTING FEMALES AT TIME OF REPRODUCTION (MM)
2.5
2.0
1.5
1.0
0
100
200
300
400
500
600
700
800
1476
NUMBER OF FEMALE SECOND INSTAR LARVAE PER TREE

Figure 6.6

The influence of the numbers of female second instar nymphs (corrected for tree size) on the size of the resulting females.


MEAN LENGTH OF RESULTING FEMALES AT TIME OF REPRODUCTION (MM)
2.5
2.0
1.5
1.0
0
1
2
3
4
5
6
7
8
9
NUMBER OF FEMALE SECOND INSTAR NYMPHS CM^{-1} STEM LENGTH
$y = \frac{x}{.706x - .143}$

ignored and the results expressed purely descriptively i.e. the influence of nymphal density on the size of the resultant female scale.

The data for the two series of trees are plotted in Figures 6.4 and 6.5 (Data in Table 17 Appendix). There is a strong curvilinear relationship for the data from trees in Series I (Figure 6.4); these data are analysed later with a correction for tree size. For the data from Series II there is no significant relationship between the number of female second instar nymphs per tree and the mean size of the resulting females although a relation is indicated (Figure 6.5). An analysis of comparable data for the two series (i.e. all above 55 second instar females per tree for the Series I and all of the Series II) indicates that results are very similar, the regression of size on numbers of second instar females being significant in neither case; the slopes are thus similar (as are the intercepts). Clearly there are no densities in Series II low enough to produce the curved relationship shown by Series I.

The best expression of the influence of second instar crowding on female size is that in Figure 6.6 where the data for Series I has been corrected for tree size (Table 18 Appendix). As there is relatively little variation a curve has been fitted by eye and the method of Lipka (1918, pages 137-139) has been used to determine the empirical equation. The relationship is hyperbolic:

$$y = \frac{x}{.706x - .143}$$

y = size of female

x = number of female second instar nymphs giving rise to the reproducing female population.

TABLE 6.1 The relationship between numbers of female nymphs, mean numbers of adult females and size.

6.1(a)

x_1 Number of female second instar nymphs	x_2 Mean number of females	y Female size (mm)
66	55.0	2.30
88	75.5	2.06
91	60.0	1.88
151	94.0	1.76
167	93.5	1.80
173	77.5	1.62
301	89.5	1.72
310	99.5	1.64
485	75.5	1.50
579	78.0	1.62

6.1(b)

x_1	x_2	y
301	89.5	1.72
310	99.5	1.64
326	116.0	1.65
354	206.0	1.39
377	18.0	1.44
380	190.5	1.93
383	142.5	1.34
386	175.0	1.91

6.1(c)

x_1	x_2	y
4	3.0	2.15
8	4.0	2.51
14	6.0	2.38
16	12.0	2.27
36	23.5	2.04
44	34.0	1.92
45	28.5	2.13
57	31.5	1.73
66	55.0	2.30
88	75.5	2.06
90	48.5	1.78
91	60.0	1.91

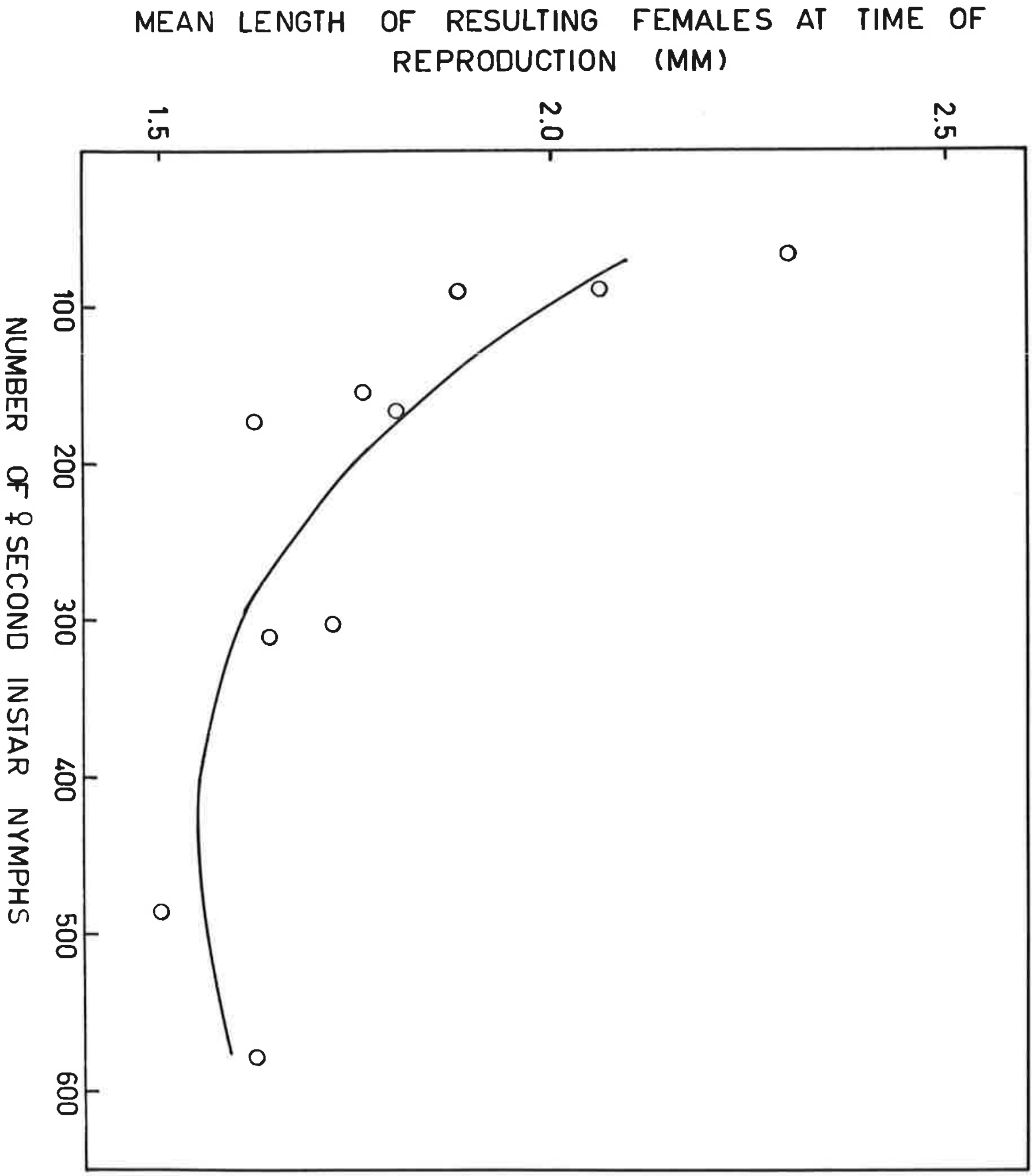
The data are now examined to try to decide whether the density of nymphs or the density of adults is the more important factor in determining the size of the females. Because mortality to the female scale occurred between the time they settled and the time of reproduction the "mean number" of females is used. This is simply: No. of females settling + No. females beginning to reproduce / 2. Some females were probably killed by the effects of high density. Others were killed in December by chrysopid larvae and spiders which entered the cages. As some of the trees grew bigger it became difficult to remove and replace the cages and some scale were killed accidentally.

It is possible to select data where there is a large variation in the number of second instar females giving rise to relatively similar mean numbers of adult females (the range for the numbers of second instars is 66-579 and for the numbers of adult females 55-99.5; see Table 6.1(a)). The length of the females is correlated with the number of female second instar nymphs ($r = -0.726$; 8 d.f.; $p < .05$) but not the mean number of adult females ($r = -0.560$). The correlation coefficient of -0.560 may indicate that the density of adult females might have some influence on their size but the most important factor is clearly the density of the nymphs.

These findings are strengthened by examining the partial correlations. When the variability due to the density of the adult females is eliminated, 52.27% of the total variability in the mean length of the females can be accounted for by the density of the second instars ($ryx_1 . x_2 = 0.723$); conversely, only 30.10% of the total variability in female size is accounted

Figure 6.7

The influence of the numbers of female second instar nymphs on the size of the resulting female when the numbers of nymphs vary greatly but the mean number of adult female scale are similar (data in Table 6.1(a)).



MEAN LENGTH OF RESULTING FEMALES AT TIME OF REPRODUCTION (MM)
1.5
2.0
2.5
NUMBER OF ♀ SECOND INSTAR NYMPHS
100
200
300
400
500
600

for by the mean numbers of adult females alone ($ryx_2.x_1 = 0.557$). Together the two variables account for 67.3% of the total variability in female size.

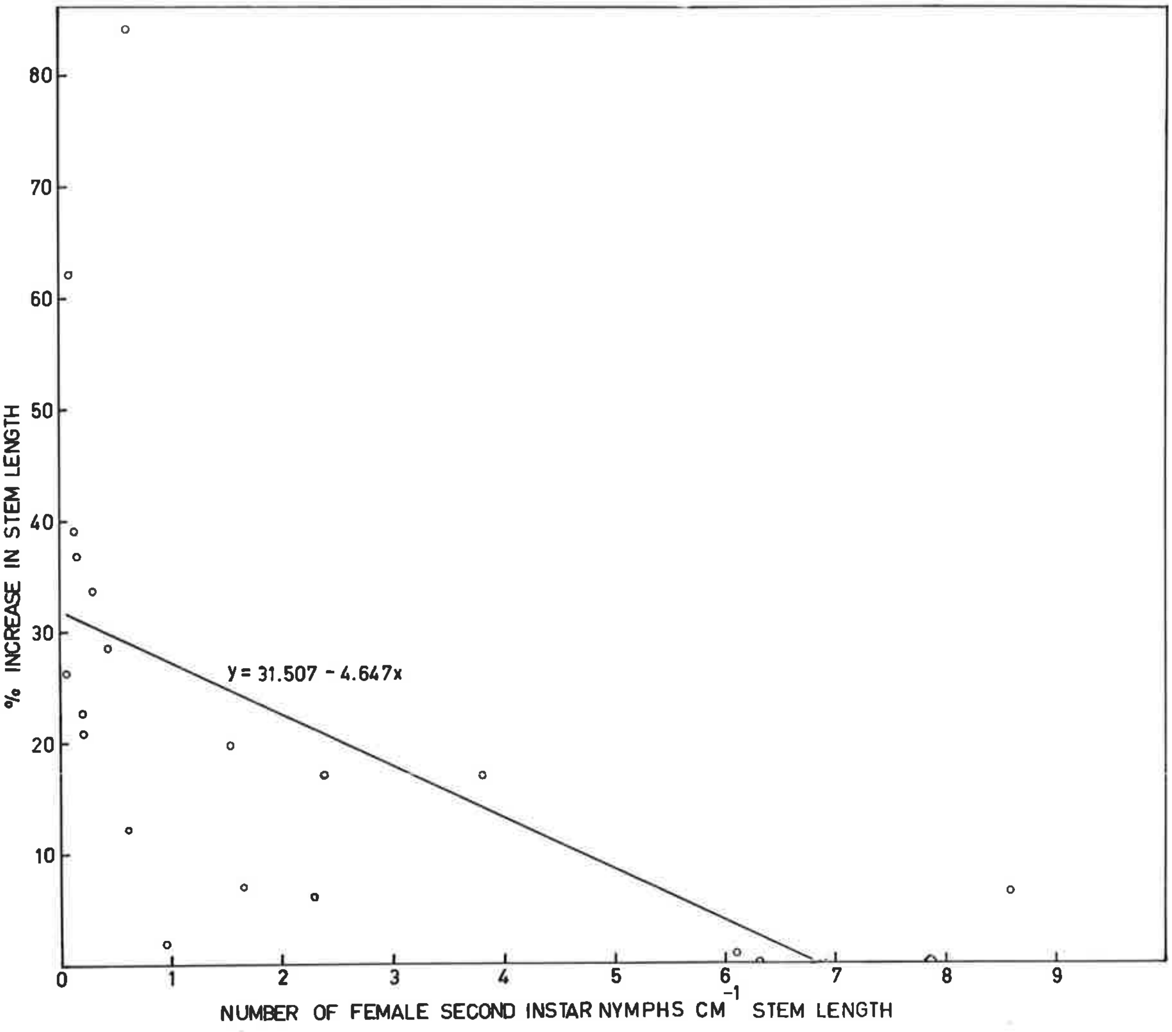
Other data that may be examined are those for which similar numbers of second instar females (301-386) give rise to highly variable mean numbers of females (18 - 190.5) (Table 6.1(b)). For these data the numbers of female nymphs do not influence female size (as is to be expected because the range of variation is limited) but neither do the mean numbers of adult females ($r = .0230$).

The final set of data, Table 6.1(c), has been chosen to examine the influence of both variables over a limited range. (Over this limited range the relationship between either factor and the size of the resulting females may be regarded as linear and this ought to give maximum discrimination to the method of partial correlations). Once again simple correlations show the numbers of second instars to be the dominating influence ($r = -0.648$; 10 d.f.; $p < .05$) and not the mean number of females ($r = -0.495$). The partial correlations confirm these conclusions. The influence of second instar density accounts for 43.5% of variability in female size ($ryx_1.x_2 = 0.660$) and the influence of mean numbers of adult females accounts for 26.4% ($ryx_2.x_1 = 0.514$). Together these variables account for 57.4% of the total variability in female size.

The hyperbolic relationship shown in Figure 6.6 is synoptic and is the outcome of several processes. The asymptote may be due either to the number of female nymphs seeded onto the tree or to the mean number of adults on the tree. If the data in Table 6.1(a) is plotted the shape of

Figure 6.8

The influence of the numbers of female second instar nymphs (corrected for tree size) on tree growth (% increase in stem and twig length).



% INCREASE IN STEM LENGTH
80
70
60
50
40
30
20
10
y = 31.507 - 4.647x
0
1
2
3
4
5
6
7
8
9
NUMBER OF FEMALE SECOND INSTAR NYMPHS CM^{-1} STEM LENGTH

the curve should be due solely to the influence of the numbers of nymphs, for the mean numbers of adult females are similar. Once again the line of best fit is curved (see Figure 6.7; $y = 2.33 - .00389x + 0.0000048x^2$ (the coefficient of x^2 is approximate); $F_{2,7} = 10.602$; $p < .01$).

The length of the female scale decreases to a certain level as the number of female nymphs increases and then the length remains approximately constant where they can maintain themselves and produce a few young but can not develop any further. Possible causes for the reduction in size are discussed later.

The fecundity of the female is related to her length (see 2.3A). To reiterate, under optimum conditions the relationship may be expressed as follows:

$$y = 309.16x - 494.74$$

where y = number of young produced

x = size of the female

Although it seems likely that the parameters may alter under different conditions (e.g. in this experiment some females smaller than 1.60 mm were producing a few young) the trends will nevertheless be similar. Thus the curve for the number of young produced against number of female nymphs would follow a similar trend to the curve for female size.

c. The influence of population density on tree growth

Tree growth declined as the population of nymphs increased. The regression of percentage increase in stem length on numbers of female second instar nymphs per cm stem length for trees in Series I is significant and linear ($F_{1,18} = 8.807$; $p < .01$; Figure 6.8). (A

TABLE 6.2 The influence of population density (number of female second instar nymphs cm^{-1} stem length) on the change in numbers of mature leaves, and immature leaves and primordia on the experimental trees.

No. second instar nymphs cm^{-1} stem length	Change in number of mature leaves	Change in number of primordia and immature leaves
.04	0	+ 11
.08	0	- 11
.13	- 2	+ 10
.15	+ 7	+ 60
.20	+ 4	+ 14
.21	+ 2	+ 12
.30	+11	+ 16
.44	+ 3	+ 4
.60	- 3	+ 25
.62	+ 6	+ 4
.94	+ 2	0
1.54	+ 1	+ 1
1.65	- 2	- 6
2.28	- 9	- 7
2.39	0	+ 16
3.81	+ 5	+ 5
6.10	- 1	- 5
6.32	- 7	- 7
6.88	- 1	- 9
8.57	0	+ 3

$r_s = .447$; $p < .05$; $.490$ $p < .05$

similar relationship exists between tree growth and the mean number of adult female *E. coriaceus*).

On two trees with high population densities parts of the tree died; these actual decreases in living stem length have simply been regarded as no increase. At the time of reproduction of the female scale all the trees were still alive but four of the trees died during the reproductive period and establishment of the young.

Besides a decrease in elongation of the stem and twigs when there were high densities of scale on the trees, there was a similar reduction in the production and growth of leaves as measured by the change in the numbers of primordia and immature leaves (Spearman Rank Correlation: $r_s = 0.490$; 20 pairs; $p \leq .05$; Table 6.2). The numbers of mature leaves were also adversely influenced by the population density of the scale on the tree ($r_s = 0.447$; 20 pairs; $p < .05$).

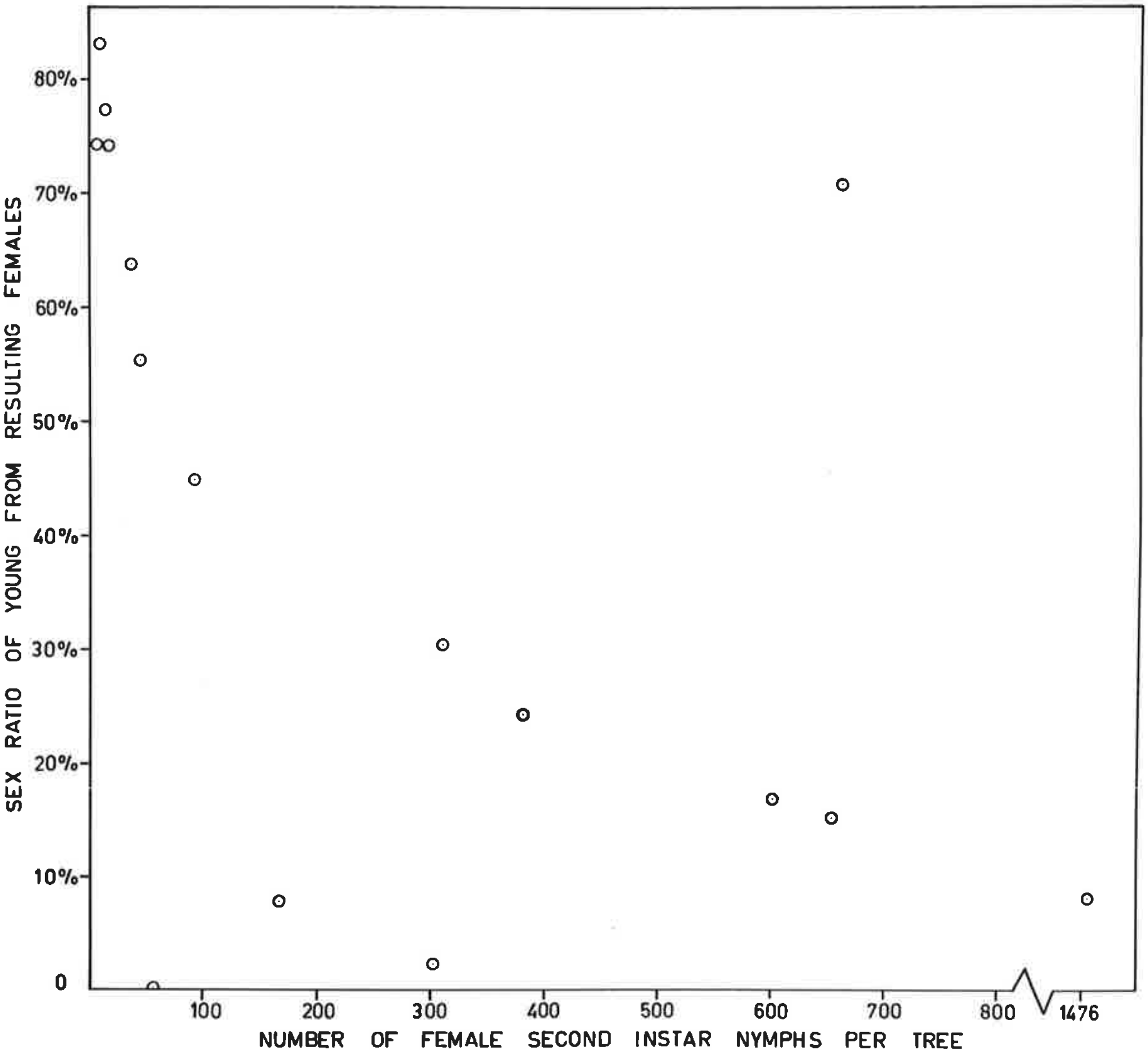
d. The influence of population density on the sex ratio of the young from the reproductive females

When reproduction began twig sections containing the reproducing female scale were cut from some experimental trees and tied onto larger uninfested trees in cages so that the young produced during the reproductive period could settle and develop. When the male pupae had been formed the sex ratio of the young was determined.

Note: Samples were removed from a total of 20 trees drawn from both series to determine the sex ratio of the young; sex ratios are therefore plotted against numbers of nymphs per tree rather than numbers corrected for tree size. Young failed to become established on four trees onto

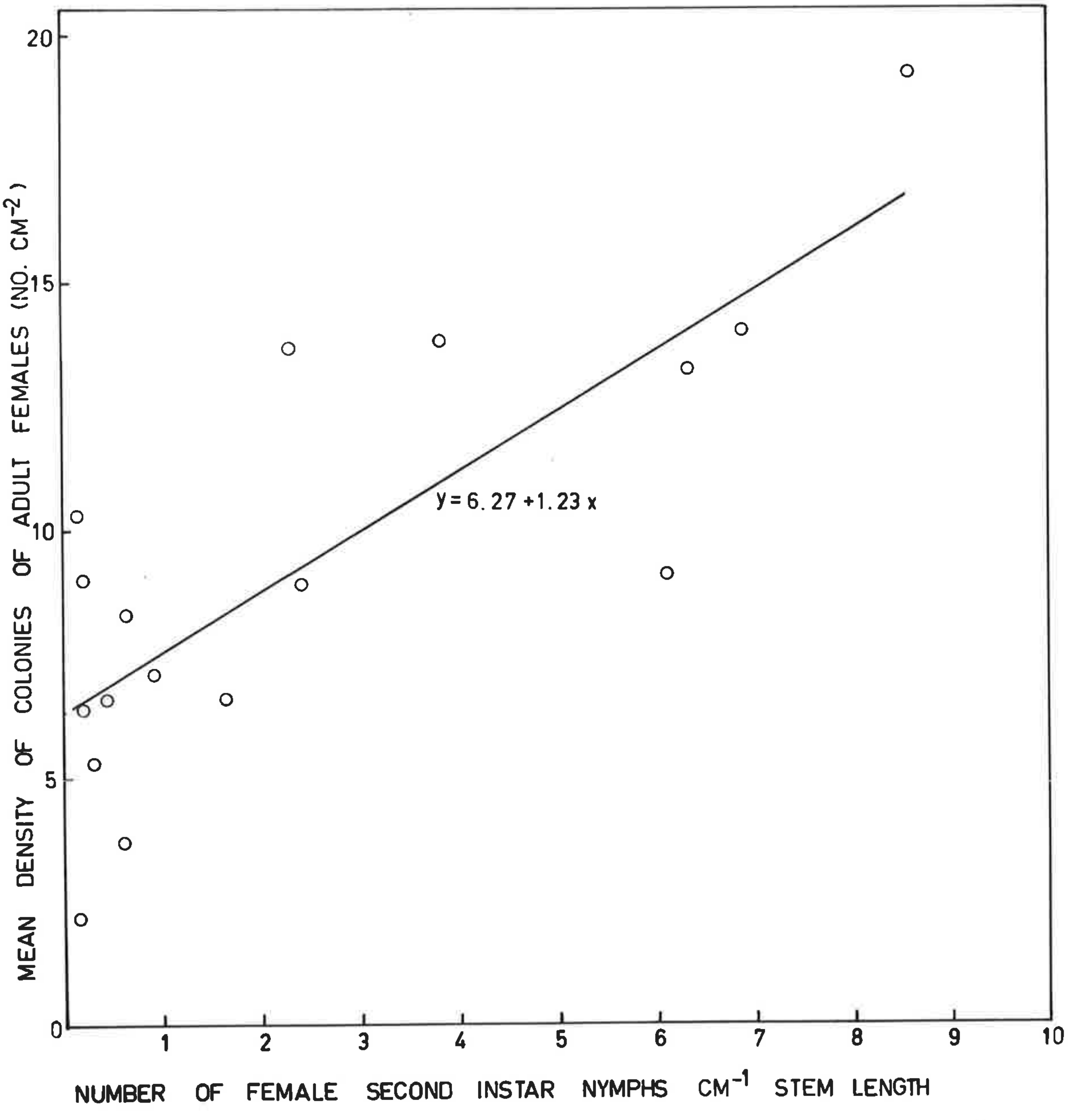
Figure 6.9

The influence of the number of female second instar nymphs in one generation on the sex ratio (% females) of the young produced by the adult females which settled from them.


80%
70%
60%
50%
40%
30%
20%
10%
0
SEX RATIO OF YOUNG FROM RESULTING FEMALES
100
200
300
400
500
600
700
800
1476
NUMBER OF FEMALE SECOND INSTAR NYMPHS PER TREE

<u>Figure 6.10</u>

The influence of the number of female second instar nymphs per cm stem length on the density of the colonies formed by the resulting females.



MEAN DENSITY OF COLONIES OF ADULT FEMALES (NO. CM^{-2})
NUMBER OF FEMALE SECOND INSTAR NYMPHS CM^{-1} STEM LENGTH
y = 6.27 + 1.23 x
0
5
10
15
20
1
2
3
4
5
6
7
8
9
10

which they were transferred.

The influence of the density of second instar nymphs on the sex ratio of the young in the next generation is shown in Figure 6.9 (Table 19 Appendix). The relationship between density of adult females and sex ratio is somewhat similar. Statistical tests failed to show any significant relationship between population density and sex ratio because of the variability in the data, but an inspection of Figure 6.9 shows a curvilinear trend.

e. The influence of the number of female second instar nymphs on the density of the female colonies

The densities of the major colonies formed by the adult females were measured on trees in Series I. The linear regression of the densities of the colonies of adult females on the number of female second instar nymphs per centimeter of stem and twig length was significant ($F_{1,15}$ = 24.957; $p < .005$. The data for two trees with very low numbers of females were omitted). Although colony density of the adults increased as the number of female nymphs that gave rise to those adults increased, the maximum density attained was only about 19 females per square centimeter which was less than that in some populations where a much smaller proportion of the total surface area of the tree was occupied by scale(Figure 6·10).

One might expect that a linear relationship between the number of female nymphs per cm of stem length and the density of the female colonies would also mean a linear relationship between the number of nymphs per cm of stem length and the number of females settling (instead of the curve shown in Figure 6.3). This was not so for even on those trees which had most female nymphs parts of the surface area were uncolonized.

6.3 Discussion

The adverse effect of crowding on fecundity is a well known phenomenon in animals (Andersen, 1957; Watt, 1960) and has been particularly well studied in aphids.

In some species of aphids colonies are formed and the rate of reproduction of the individuals in these colonies varies with the size of the colony. Way and Banks (1967) and Way (1968) found that the rate of multiplication in colonies of 4 to 8 adult apterae of *Aphis fabae* was significantly greater than in smaller or larger colonies. In colonies of the optimum size the aphids condition the area of leaf on which they feed, presumably by their salivary secretions, which acts as a physiological sink and competes with growing parts of the plant for nutrients (Way and Cammell, 1970). Aphids in such an aggregation are thus better fed than those which feed singly (Way and Cammell, 1970; Dixon and Wratten, 1971).

The optimum colony size is soon exceeded and the fecundity of the adults produced in these larger colonies decreases. This decrease in fecundity may have its origins in either the nymphal or adult stage of the aphid and may be caused by increased jostling as the colony size increases, by competition for food or by both. Way and Cammell (1970) found that solitary *Brevicoryne brassicae* reared on the opposite side of the leaf to overcrowded aggregates were less fecund than those reared opposite optimum sized aggregates or those reared entirely on their own, and this decrease in size was due to competition for food. Way and Cammell considered that reproduction in B. brassicae may also be slowed down by jostling even though nutrition is adequate. Murdie (1969(a)) found that smaller and lighter adults of A. pisum were produced by crowding in the nymphal stages and this was due to the interactions between the nymphs rather than deterioration in the host plant. These lighter adults produced fewer larvae than larger adults reared under uncrowded conditions (Murdie 1969(b)). Bonner and Ford (1972) showed that crowding large adult Megoura viciae, which had been reared in isolation as nymphs, had a pronounced deleterious effect on their fecundity and these adults produced fewer young than aphids which had been crowded all their lives.

Dempster (1968) found crowding in the adult broom psyllid Arytaina spartii caused a great reduction in fecundity (larval crowding had little effect).

The general trend is therefore for a lower fecundity of aphids produced in crowded colonies.

Crowding has been established as a factor of prime importance in the production of alate aphids. In some aphids e.g. peach aphids on chrysanthemums (Wyatt, 1965) the emigration of the alates is sufficient to stabilize the population without a decrease in the birth rate. In B. brassicae however this is not the case for as the aggregate grows in size the percentage of adult apterae remains remarkably constant in colonies of 100 to over 5,000 (Way, 1968) and the slowing down in the rate of increase in the population is caused by both a decrease in fecundity and an increase in the production of alates. The production of alates is a complex process and may involve both jostling and a deterioration in the quality of the sap ingested. Way and Cammell (1970) found that two sorts of alates of B. brassicae were formed. Early in the life of the colony a large form was produced caused by competition for space when the food supply was probably adequate, and a small form was produced late in the life of the colony when the quality of the sap declined and induced restlessness.

Not only winged aphids migrate. Way and Banks (1967) found that nymphs and apterous adult Aphis fabae walked off bean plants when the population density was high. Sanders and Knight (1968) found that the population of Pterocomma populifoliae reached a peak in numbers on small caged big-tooth aspen suckers and then declined; the decline was due entirely to aphids walking off the plants. Boakye (1973) found that apterae and nymphs of Hyperomyzus lactucae left sow thistles. Macrosiphum rosae walk away from dense colonies on rose buds (Maelzer, 1975).

Way (1968) and Way and Cammell (1970) come to the following conclusions as to why some species of aphids form colonies. Initially aggregation is beneficial for physiological sinks are formed, the aphids are uncrowded and the rate of reproduction is maximal. Thus a substantial colony is produced in the shortest possible time. This stage is soon passed, then competition is induced at an artificially early level. The rate of reproduction slows and migration increases thus protecting the host plant (as much as possible) from being over-exploited but enabling the species to spread widely and infest new plants and also enabling the original colony to exist as long as possible. Way and Cammell (1970) show that the formation of discrete colonies protects the plant and yet enables the aphids to exploit it more efficiently. When a population of B. brassicae was spread over the four leaves of a plant it produced fewer alates per square centimeter of colonized leaf and a lower overall biomass than a similar population confined on a single leaf. At the end of the experiment the plant on which all leaves were colonized was dead, whereas the three uncolonized leaves of the other plant were still in good condition.

Dixon (1971) demonstrated that infestations of aphids could seriously affect the growth of woody plants. He considered that the saliva the sycamore aphid (Drepanosiphum platanoides) injected into the sycamore was the chief reason for the decline in growth (Dixon 1971(a)). The saliva of homoptera is known to contain substances which influence the growth of plant tissue (Miles, 1973) and the secretions can be translocated throughout the plant (Lawson et al., 1954). Dixon (1971(b)) also found the lime aphid (Eucallipterus tilliae) reduced the growth of roots of the lime and he considered that this was probably due to the removal of photosynthates in the honeydew of the aphis (see also Llewellyn, 1972) but could not rule out the possibility that secretions from the saliva of the aphids were translocated to the roots and affected their growth.

Further investigations by Forrest et al. (1973) and Hussain et al. (1973) showed that infestation of Myzus persicae on radish seedlings reduced leaf and cotyledon growth, root growth and reduced the amount of sap exuded to 4% of that found in uninfested plants. Aphids became restless after feeding for some days on these seedlings and this they considered most likely due to the small volume of sap available. The very small quantity of sap could not be explained by the decrease in root growth *per se*. The authors considered that it was due either to the damage of the phloem cells (caused by the aphids feeding) which prevented metabolites produced in the leaves from reaching the roots, or directly to the influence of the salivary secretions on the root functions.

With these findings in mind the experiments on *E. coriaceus* can now be examined.

Physical crowding alone may decrease the fecundity of female *E. coriaceus* (6.1D). Other factors must also be important for the smaller adults measured on the caged tree with the highest population (over 50,000) were not touching their neighbours and the colonies produced on the trees in Kuitpo Forest were also not dense enough to cause mechanical crowding.

If the work on aphids is used as a basis, the decrease in size may be caused by competition for food, by a decline in the quality of the host plant, or by the interaction between the active stages before they settle (for once they settle and secrete the test they do not move). The scale which developed on the end of the twigs (a site not usually colonized) on the caged tree with the largest population, were significantly larger than those which developed further down the twig at the usually preferred site. Both came from the same population as nymphs, so the differences can not be attributed to interaction between the mobile stages. Although none of the scale which were measured touched their neighbours, the smaller scale (from further down the branch)were in the midst of very extensive colonies which covered most of the branch. There was thus likely to be either competition for food or a decrease in the quality of the sap; the latter could be caused by the accumulation of the salivary secretions of the scale.

Metabolites in the phloem (which are the food of the scale) are the products of photosynthesis and thus those areas nearest the leaves, the ends of the twigs, are the first to receive the enriched phloem sap. Ordinarily the flow of metabolites would increase from the tip to the base of the branch because of the accumulation of photosynthetic products channelled into the main conducting elements in the branch by secondary branches.

With large colonies of scale covering most of the branch the metabolites will be extracted (by the scale) and the quality of the phloem will decrease as it passes down the branch. The scale which settled at the tips therefore received the best supply of food on the tree with the large population. This was still inadequate for full development, however, because these females were smaller when they reproduced than those females on trees with low populations.

The dominant influence of the numbers of second instar nymphs on the sizes of the resulting females is more difficult to understand. Certainly the influence of the scale would be exaggerated by the fact that light was cut down by the cages (which had a fine gauze in order to exclude parasites) but even so the plants with few scale grew vigorously in the cages. Most of the scale were very well attended by ants and as has been shown the rate of excretion of honeydew for first instar nymphs is about 1.5 drops/nymph/five minute period. Each nymph may excrete 144 drops in a 8 hour day and a population of 100 nymphs could excrete 14,400 drops per day, which is likely to be a great drain on the plant. It seems that long lasting changes occur in the plant for even when a small mean number of adult females arise from a large number of nymphs the latter are still most important in determining the size of the scale. This is perhaps due to the effects of their saliva on the plant. Leaves showed premature senescence and there was a decrease in the production of immature leaves and primordia, as well as in shoot growth on trees infested with many nymphs.

There are probably several reasons for the migration of the active stages from the tree. The migration from Obs. 1 in November 1971 occurred when much of the surface area of the tree was still uncolonized and the tree certainly showed no external signs of stress. It was clearly a suitable site for the development of the scale, for a large population of females (21,600) settled and reproduced in January 1972. Although their size was smaller and they formed denser colonies than those scale on a nearby tree with a lower population they were otherwise normal. Many of the crawlers produced were forced to crawl over extensive colonies of nymphs already settled and the interactions between them may have increased their restlessness, tending to make them walk further and leave the tree. Way and Banks (1967) noticed that emigrating young adult apterae of <u>Aphis fabae</u> remained restless and did not settle even on a suitable plant. They had an initial wandering period very much like the migratory period of the alates.

A deterioration in the quality of the host plant is also known to induce restlessness in aphids causing them to migrate. This almost certainly occurs in _E_. _coriaceus_ (see 6.1A). Both nymphs and young females which have not secreted their test can withdraw their stylets and move away if conditions are not suitable. The reason for the decline in numbers of females remaining on trees at Kuitpo when there were very large numbers of second instar nymphs on them (Figure 6.3) may be either a deterioration in the quality of the tree, caused by the initial large population of nymphs, or by the interaction between the newly moulted females looking for a place to settle. The former seems the most likely explanation for parts of two of these trees died during the experiment.

Andersen (1961) reviewed the literature on the influence of population density on the sex ratio. He was concerned primarily with the influence of the density under which young were reared on their sex ratio when they reached maturity. Although some deviations from 1:1 sex ratio in organisms with X-Y chromosomes and random assortment occur such changes are rare and usually not pronounced. Only in organisms with unorthodox sex determining mechanisms are drastic changes in the primary sex ratio possible. Andersen cites work with plant and animal parasitic nematodes, copepods, cladocera where the proportion of females in the young decrease with increasing density. Ellenby (1954) demonstrated conclusively that the % males in primary sex ratio of _Heterodera_ _rostochiensis_ (the potato eelworm) increased as the density of the population increased. Female _E_. _coriaceus_ which develop under crowded conditions produce a greater proportion of male young than those developing under normal conditions. This must be a powerful method for preventing population growth, for despite the variability, the reduction in % females shown in Figure 6.9 is very marked. One advantage of producing many males, apart from suppressing population growth, may be that there is a greater likelihood that females which have dispersed (wandering off the tree when the density is high and settling on trees nearby) will be fertilized. Considering the unusual sex determining mechanisms in coccids (2.4) reduction in the sex ratio at high density may well be a widespread feature of the group.

E. coriaceus clearly has many features in common with aphids in the way it attempts to control population growth. Emigration from crowded trees occurs, and females developing under crowded conditions are of a smaller size and therefore less fecund than uncrowded individuals. It differs from the aphids in being able to control the sex ratio of the young produced. Although fecundity may be restricted via the colony this occurs only when the population density on the trees is very high and even then, as demonstrated by the trees at Kuitpo, this does not invariably occur.

That E. coriaceus has less refined mechanisms for limiting population growth than some species of aphids is not surprising. It utilizes a greater proportion of its host plant, is more severely attacked by natural enemies and has a much lower capacity for increase (Laughlin, 1965) than most species of aphids. Self-limiting mechanisms were rarely found in populations on large trees but may be an important feature of the ecology of scale on small trees.

CHAPTER 7 Discussion

When *E. coriaceus* was introduced into New Zealand it quickly covered a very large area (1.2) demonstrating that even though the adult females are sedentary the species can nevertheless disperse widely and quickly. This is because the young may be dispersed by the wind.

After the introduction of *R. ventralis* the outbreak of *E. coriaceus* declined rapidly and the population stabilized at a low level. The situation seems very similar to that found in Queensland where the prickly pear (*Opuntia* spp.) is destroyed by the moth *Cactoblastis cactorum* (Dodd, 1940). A typical "spotty distribution" is formed which is the end result of the interaction between an efficient specific predator with wide powers of dispersal and a more sedentary prey (Nicholson, 1958). Patches of the host escape and may reach high numbers locally before they are found by the predator which then builds up in numbers very quickly and often completely destroys the local population of the host.

In Australia the ecology of the scale is more complex. Although large tracts of Australia are covered by the food plant which grows in almost pure stands (for *E. coriaceus* is found on many species of eucalypts) the population of the scale nevertheless remains stable for no outbreaks have been recorded in Australia and scale are found in low numbers. The most obvious reason that the scale are always rare in relation to their food is that they are attacked by many species of predators and parasites.

E. coriaceus may be dispersed over long distances by the wind, but in local populations the scale has more limited powers of dispersal than its natural enemies. The scale is mobile for three brief periods in its life and dispersal at these times is by the scale walking from tree to tree or by relying on being blown by the wind. On the other hand, all the predators and parasites are winged in the adult stage. All the predators (at the time they are active) have a shorter generation time than the scale. One might therefore expect that populations of E. coriaceus would remain small in relation to the area they could occupy (Andrewartha and Birch, page 477, 1954) and this was generally true. Indeed with such formidable disadvantages it is a wonder that the scale survives at all and relatively stable populations occur only because of the attendant ants.

7.1 The importance of ant attendance

Ants give stability in two ways; firstly by protecting the scale, and secondly by allowing a diversification of the predator complex. Ants do not confer absolute protection on E. coriaceus for R. ventralis is still a predator of major importance but as has been shown in 4.3 without the ants R. ventralis would completely destroy local populations of the scale, such as appears to be the case in New Zealand where ants are not common (Zondag, pers. comm.).

Predation by R. ventralis on E. coriaceus in the absence of ants is unusually efficient. All the ant-free populations were eventually destroyed (4.6). The only reason that populations of E. coriaceus have been able to exist continuously for three and a half years on some trees seems to be the protection given by the attendant ants. The coccinellids were efficient in destroying the prey even at low densities (see 5.3F).

At high densities 60% of the living female scale contained eggs of the coccinellid (5.3Eb) and when these hatched the large numbers of larvae destroyed the scale. Two natural populations, which were not part of the survey, were completely wiped out by predation by *R. ventralis* in August 1971 and 1972 (larvae in large numbers were seen leaving the trees when all the scale had been killed). Thus even when ants can tend the scale but the weather is cold *R. ventralis* may still completely destroy populations. The efficiency of *R. ventralis* when there are few scale on a tree may be due to the habit of the scale forming colonies so that even if the population is low the individuals are often still aggregated.

Ants also allow a more diverse entomophagous fauna. With ants present in November 1972 small areas of nymphs survived. Thus not only the scale population in the area continued but so did the populations of the other natural enemies. In the absence of *R. ventralis* and in the warmer weather, populations of these natural enemies adapted to living with ants were able to increase and, together with the lower fecundity of the female scale in summer (3.4), keep the population of *E. coriaceus* at a low level.

Bradley (1973), working in Manitoba, found the spread of the coccid *Toumeyella numismaticum* restricted by predation by the coccinellid *Hyperaspis congressis*. The scale occurred in isolated pockets where they had survived for a long time and where large ant populations had developed. When spread beyond these pockets the scale were tended by a few ants but these were not enough to prevent the coccinellid destroying the scale. The density of coccinellids was maintained because a few survived on the ant-attended trees where there were many scale and these dispersed throughout the forest. Ants are very widespread in the areas of South Australia in which I worked (see 4.1B) and it seems very unlikely that the spread of *E. coriaceus* would be restricted in the above manner.

7.2 The natural enemies of *E. coriaceus*

The natural enemies of *E. coriaceus* are not only diverse in terms of numbers of species (at least 16) but are even more remarkable for the number of orders they represent (Neuroptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera) and the diversity of their habits. The following properties of the *E. coriaceus* system probably lead to such diversity:

1. The female scale are sessile.
2. The female scale are covered in a test.
3. The females form extensive colonies as well as occurring in small groups or as single individuals.
4. The scale are to be found throughout the year.
5. The scale are attended by ants.

The first two qualities mean that two universes for entomophagous insects are formed. The free ranging predators wander over the surface of the scale whilst beneath the test ectoparasites, such as *P. beneficia*, develop and larvae of *S. melanochra* form mines in colonies of the scale. The larval stages of *P. beneficia* and *S. melanochra* are highly specialized to lead a concealed mode of life beneath the scale, the most obvious benefit being the lack of interference by ants.

Even in the free ranging predators there is a great deal of diversity and this may be due chiefly to the attendant ants. The predators may be divided into two groups. The first very minor group of predators (*Melangyna* sp. and *Leis conformis*) was seen when ants were absent or present only in very small numbers. They feed chiefly on other species of homoptera and have no adaptations to life with ants. The second and most important group of predators are those which come into conflict with the attendant ants but have behavioural adaptations (*Rhizobius ventralis* and some of the more uncommon species of coccinellids) or morphological adaptations (*Catoblemma* spp. and *Cyclotornia* sp.) to overcome the protective influence of the ants. These adaptations are successful in varying degrees in protecting the predators.

As the scale are present throughout the year the seasonal separation of the most important natural enemies occurs. *R. ventralis* and *Catoblemma* were the most important free ranging predators and I saw very little competition between them. *Catoblemma* larvae appeared in some numbers in late November and early December which was the time that the population of *R. ventralis* declined rapidly. *Catoblemma* larvae fed on the scale throughout the summer but became uncommon in April which was the time *R. ventralis* began to appear again. *Catoblemma* appeared to be much better adapted to life with large numbers of ants than *R. ventralis* but probably had a winter diapause. *R. ventralis*, by virtue of being able to feed and develop in cold weather, was able to thrive when ants were in low numbers. By feeding at night the larvae and adults avoided the ants even in warmer weather in spring. The rarity of *R. ventralis* in summer may have been caused by a lowering of fecundity due to high temperatures but most probably was due to the ants which, in summer, attended the scale at night and prevented *R. ventralis* from feeding.

The activities of *R. ventralis* and *Aphycopsis* spp. also did not overlap. Even in populations in winter where relatively few scale were eaten by *R. ventralis* the rate of parasitism was very low suggesting that their rarity is due to cold weather or some factor associated with it, and not because the coccinellid eats many scale containing developing parasites. *Chrysopa ramburi*, *P. beneficia*, *S. melanochra* and minor coccinellids were of relatively little importance compared to *R. ventralis*. *Aphycopsis* spp. are the major natural enemies in summer and in both years they attacked nearly all populations of scale often causing heavy mortality. *Catoblemma*, *P. beneficia* and *S. melanochra* were more sporadic.

If *R. ventralis* was the only predator and ants attended the scale, greater instability in the scale population would result. The coccinellid is absent during the summer and without some check populations (such as on tree A6 in November 1972 to January 1973) would reach very large numbers before they would be reduced next winter. It seems inconceivable, however, on the experiences in New Zealand, that *E. coriaceus* could ever escape from *R. ventralis* (even if it was the only predator) and kill trees over a wide area.

If the other natural enemies were present but *R. ventralis* was absent the population of *E. coriaceus* would be even more unstable and might reach high numbers for although the other natural enemies may reduce large populations of scale their action is largely restricted to the summer months. It has been shown that, in the absence of *R. ventralis*, very pronounced population increases in numbers of scale can occur from August to November and November to January. In 1972 one such population (Obs. 1) remained at a high level and was not greatly reduced even by the combined action of hymenoptera, *P. beneficia*, *S. melanochra* and pronounced density-induced negative feedback mechanisms. This population would almost certainly have been greatly reduced by *R. ventralis* in September 1972 if it had not been destroyed for experimental purposes. A similar population in January 1973 however was completely destroyed by hymenoptera and *Catoblemma*.

The population of the major natural enemies, *R. ventralis* and *Aphycopsis* spp., were highly variable with regard to time but exhibited regularity in the time peaks of attack occurred each year and in the proportion of scale destroyed. Those natural enemies present most of the year, *P. beneficia* and *S. melanochra*, apparently had only a very minor influence on the populations of the scale.

The natural enemies themselves support parasites and hyperparasites. One interesting feature of this complex is that whilst two species of the genus *Aphycopsis* are primary parasites of *E. coriaceus* another species parasitizes *R. ventralis* larvae. Similarly *Quaylea* sp. is not only a hyperparasite of the encyrtids but is a primary parasite of *P. beneficia*. This trend of the same species (or different species) in a genus of hyperparasites attacking primary parasites of the homopteran host, as well as the natural enemies and their parasites, is well known among hyperparasites of aphids e.g. in the genera *Dendrocerus* and *Pachyneuron* (Takada, 1973; Kamijo and Takada, 1973).

7.3 The importance of intra-specific competition

In the study area at the Waite Institute populations were studied on trees about 2 m high or larger. The scale had to complete at least two consecutive generations under highly favourable conditions before the population became large enough to occupy a sizeable proportion of the surface area of the tree and before density induced negative feedback mechanisms operated. This rarely occurred because of the effectiveness of the natural enemies.

Many populations in the wild, however, live on smaller seedlings and suckers and must frequently occupy most of the surface area available (6.2). When this occurs all the females do not settle and large numbers of the active stages walk off the tree (6.2Ba); the size of these females when they reproduce is related to the population density, smaller and less fecund females being produced from larger populations (6.2Bb); the sex ratio of the young, although variable, apparently also changes from being predominantly female under conditions of low crowding to predominantly male under crowded conditions (6.2Bd). These processes slow down the rate of growth of the population. The levelling off in the number of females settling on a tree is probably particularly important for even in cages many of these survived to produce a few young. In natural populations these females would be subject to mortality from predators and weather and under these conditions many would die, not only relieving the pressure on the surviving females but also on the tree which would be growing more vigorously anyway.

Thus under natural conditions the intraspecific processes enable the scale population to continue for long periods on small trees and also to protect the trees, to some extent, for overexploitation.

7.4 Weather

The weather may influence the numbers of the scale either by acting on the population of scale, by acting on the populations of natural enemies, or by altering the activities of the ants causing them to give greater or less protection to the scale.

Weather may act on the scale themselves in two ways. The scale, particularly the immature stage, may be killed by harsh weather (rain, winds or high temperatures). Weather may also influence the population by altering the physiology of the host tree. White (1969, 1974) has postulated that outbreaks of phytophagous insects, both sap sucking and leaf feeding, often occur when the trees are stressed by weather. Under such conditions the level of nitrogen in the sap increases as does the survival of the immature stages of the phytophagous insect.

White (1966) discusses very large populations of *E. coriaceus* on several trees in the south-east of South Australia. These populations killed several large gums (*E. cornuta*, a native of Western Australia) which normally grow in a 40" - 60" rainfall but were grown near Keith, which has an average rainfall of 18" a year. The trees survived well for a long period when rainfall was above normal but succumbed to the scale in a drought year. He concluded that the increase in the population of the scale was caused by the increased favourability of the sap. While this is possible, there may be other explanations, e.g. in dry years ants may attend the scale more assiduously.

Even if the survival of the young of E. coriaceus were enhanced by conditions of stress on the host tree major widespread outbreaks still do not occur, presumably because of the poor powers of dispersal of the scale relative to its natural enemies. Females of Cardiaspina densitexta, the psyllid which White worked on, are winged and highly dispersive over considerable distances (White, 1970(b)); furthermore predators and parasites are of little importance in the ecology of this species (White, 1966). It is not surprising, therefore, that very large outbreaks (presumably triggered by an improvement in the quality of the sap) of this psyllid have been reported (White, 1966; 1969).

7.5 Conclusion

Even in the relatively uniform study area at the Waite Institute populations of the scale were capable of showing marked differences in trends at any time. Some were heavily attacked by predators whilst others escaped predation either because they were not found by predators or because they were well attended by ants.

Although the scale was not studied in the wild observations indicate that the populations here too exhibit marked independence. This is not surprising when one considers the complexity of the situation. Predators may or may not find the scale, different predators are active at different times of the year and different species of ants may tend the scale and modify the action of the natural enemies in different ways.

The most important question is what influence do the populations of the scale have on one another? The founding of a new population is clearly an important event but is essentially migrants from an established population settling and surviving on one of the many uninfested trees. Once a colony is established the likelihood of the original, or other established populations influencing the newly formed one by interchange of scale is probably very small unless the populations are very close and scale can walk from one to another. The only way therefore that most populations influence one another is via the predators which can move from one population to another. In this way populations in a restricted area influence one another greatly. The influence of widely spread populations on one another, however, depends to a large extent on the specificity of the predators.

Although *R. ventralis* and *Catoblemma dubia* and *C. mesotaenia* have been recorded attacking coccids introduced into Australia (Wilson, 1961) and doubtless also feed on native coccids beside *E. coriaceus*, the latter scale must be considered the most important source of food for these predators in South Australia because of its abundance (relative to other indigenous coccids). The adaptations of *R. ventralis* to life with *E. coriaceus* surely also marks the scale as a food source of primary importance for the coccinellid. Thus even widespread populations may have a significant influence on one another.

In any future study the population dynamics of the scale might well be examined by assessing changes in the number of infested trees rather than the numbers of scale on them. The following questions could be asked:

(a) How often are new populations founded and what factors cause variations in the rate of establishment? One might look to weather, topography, age of the trees and prevailing winds as possibly important influences.

(b) How long do populations on trees persist?

(c) How often are populations extinguished and what influence do the different species of predators, different species of ants and tree size have?

(d) In the present study few large trees were seen infested with the scale. Is this because I did not look carefully enough or is it because large trees are unfavourable, either physiologically or for other reasons? In New Zealand very large gums were attacked (Kirk, 1908), and White (1966) reports that large gums in unfavourable sites in South Australia were killed; this may indicate that large trees in unnatural situations are more prone to attack than large trees occurring naturally. On the other hand predators were absent in New Zealand and other factors may have influenced the populations White saw.

(e) Why do scale form colonies? Are the reasons physiological? Large numbers of scale attract large numbers of ants and therefore scale in a colony may be better protected than the same number of isolated individuals.

(f) How often does intraspecific competition occur in natural populations?

(g) I have suggested that ant attendance is always adequate; is this in fact so?

(h) Is the survival of the immature stages enhanced by increased nitrogen in the sap when trees are stressed?

The ecology of _E. coriaceus_ should be studied with the overall view of den Boer (1971) in mind. Perhaps the frequency of occurrence of events is more important than their quantitative impact; thus the ecology of the scale could be studied over a broad area and the probability of important and clear cut events occurring such as the founding of new populations, the discovery of a population by predators or parasites of different species and the chance that they will extinguish a population, may be more important than the actual quantitative estimates of percentage survival and mortality.

APPENDIX

TABLE 1 Code numbers and species of trees mentioned in the text.

Code Number	Species of *Eucalyptus*
Obs. 1, Obs. 2, Obs. 3, Obs. 4	*E. cladocalyx*
A1, A2, A6, A7, NA1, NA2, NA6, NA7	*E. leucoxylon*
A3, A8, A11, NA3, NA8	*E. camaldulensis*
A4, A9, NA4, NA9	*E. odorata*
A5, A10, A12, NA5, NA10	*E. viminalis*
1842A	*E. triflora*
1908B	*E. platycorys*
1954B	*E. normantonensis*
1821C	*E. erythrandra*

TABLE 2 Number of female scale examined to determine causes of mortality.

Tree	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Alverstoke								
Obs. 1	191	50	299	637	843			
Obs. 2	565	50	118	232	107			
Obs. 3	46	50	-	-	-			
Obs. 4	-	-	374	410	891			
Trees from ant experiment								
A1						108	29	-
A4						81	24	-
A6						326	179	-
A8						226	14	-
A10						229	97	77
A12						-	92	212
Mallee Block								
1842A	-	238	53	92	380	199	130	21
1821C	-	219	21	-	-	-	-	-
1954B	-	-	50	28	47	230	77	-
1908B	-	-	137	77	67	123	149	25
E. erythronema	-	-	-	-	-	-	-	52

TABLE 3(a) The influence of density (number per disc) on the settling rate of crawlers of *E. coriaceus*, and the proportion that drowned, 6 hours after seeding.

Initial number of crawlers per disc	1	5	10	15	20	30
Total number of crawlers seeded onto discs	50	50	100	150	180	300
Number of crawlers settled after six hours	28	32	72	117	136	258
Number settled as a % of the total seeded	56.0%	64.0%	72.0%	78.0%	77.2%	86.0%
Number of crawlers drowned after six hours	12	7	9	13	26	14
Number drowned as a % of the total seeded	24.0%	14.0%	9.0%	8.7%	14.4%	4.7%

TABLE 3(b) The influence of density (number per disc) on the percentage of those nymphs settled after 48 and 96 hours which had begun to secrete wax.

Initial number of crawlers per disc	1	5	10	15	20	30
A. Number settled after 48 hours	27	32	64	124	128	250
B. Number secreting wax after 48 hours	13	20	41	87	68	132
B as a percentage of A	48.2%	62.5%	61.4%	70.2%	53.1%	52.8%
C. Number settled after 96 hours	27	35	71	121	93	239
D. Number secreting wax after 96 hours	23	32	50	110	90	182
D as a percentage of C	85.1%	91.4%	70.4%	90.9%	96.8%	76.2%

TABLE 4 Seasonal variation in the mean density of colonies of female *E. coriaceus*.

Time of Sampling	Mean Density ± 1 Standard error	Number of trees sampled
August 1971	14.8*	3
November 1971	18.0 ± 1.35*	4
January-February 1972	20.3 ± 2.50	5
March-April 1972	45.4 ± 5.78	5
August 1972	16.2 ± 1.92	7
November 1972	16.1 ± 1.90	9
January 1973	19.3 ± 1.49	6
March 1973	41.9 ± 3.97	5

* Contains some colonies where density was estimated by eye.

TABLE 5(a) Influence of length of female scale at time of reproduction on number of offspring produced. Females on leaf discs at 25°C November 1971.

Length of female scale in mm	Number of offspring
2.13	70
2.25	197, 203
2.38	166, 220, 243, 256
2.50	193, 273, 289, 303
2.63	226, 236, 293, 297, 355, 355, 562
2.75	322, 477, 496
2.88	393, 450
3.00	321, 460, 523
3.13	402
3.63	546

TABLE 5(b) Influence of length of female scale immediately before reproduction on the number of embryos contained. November 1971.

Length of female scale in mm	Number of embryos
2.13	105
2.39	224
2.53	117, 203
2.66	215, 227, 230, 292, 297, 320, 375
2.79	345
2.93	300, 338, 360, 397
3.06	305, 333, 375, 398, 405
3.19	380, 417, 450
3.33	378, 405, 462, 496, 591
3.46	580

TABLE 6(a) Length of adult female *E. coriaceus* in different seasons. Means (± standard error) for samples removed from survey trees near Alverstoke Orchard.

Time of Sampling	Obs. 1	Obs. 2	Obs. 3	Obs. 4	Overall Means
August 1971	3.05(±.13)^{3}	2.96(±.12)^{3}	2.94(±.12)^{3}	---	2.98
November 1971	3.17(±.09)	2.80(±.07)	---^{1}	---	N.S. 2.99
January 1972	1.87(±.08)	2.35(±.09)	---	2.58(±.09)	* 2.27
March 1972	1.70(±.04)	2.10(±.19)	---	1.84(±.06)	N.S. 1.88
August 1972	2.59(±.09)	3.08(±.03)	---	2.89(±.08)	* 2.85

The following measurements were made on the trees seeded for the experiment on protective effect of ants.

Time of Sampling	Tree A10	Tree A12	Tree A6	Tree A4	Tree A8	N.S.
November 1972	3.26(±.07)	3.00(±.07)	3.19(±.10)	2.73(±.10)	2.84(±.09)	3.00
January 1973	2.36(±.09)	2.74(±.05)	2.53(±.08)	1.83^{2}	2.89^{2}	* 2.47
March 1973	1.55(±.05)	1.99(±.06)	---^{1}	---^{1}	---^{1}	* 1.77

NOTES

1. Population of scale completely destroyed on this tree.
2. Only one colony surviving or survivors in only one of the colonies removed at random.
3. From these populations bark samples were not removed but scale were taken at random (i.e. only one sample).

* Means successive values are significantly different ($p < .05$).

N.S. Not significant

TABLE 6(b) Length of adult female *E. coriaceus* in different seasons. Means (± 1 standard error) for samples removed from survey trees in the Mallee Block.

Time of Sampling	1848A	1908B	1954B	Overall Means
January February 1972	2.36(±.10)	2.03(±.14)	2.28(±.14)	2.22
				N.S.
March April 1972	2.10(±.09)	1.48(±.04)	2.17(±.04)	1.92
				*
August 1972	2.67(±.09)	2.44(±.11)	2.97(±.10)	2.69
				N.S.
November 1972	2.87(±.02)	2.61[2]	2.87(±.02)	2.78
				*
January 1973	2.12[2]	1.96[2]	—[1]	2.04
				N.S.
March 1973	1.77[2]	1.54(±.03)	—[1]	1.66

NOTES

1. Population of scale completely destroyed on this tree.
2. Only one colony surviving or survivors in only one of the colonies removed at random.
3. From these populations bark samples were not removed but scale were taken at random (i.e. only one sample).

* Means successive values are significantly different (p < .05)

N.S. Not significant

TABLE 7 Sampling data for trees where stratified sampling method was used.

Tree and date	N_1	y_{1a}	s_1^2	n_1	$\bar{y}_{1b}$	Pop	N_2	$\bar{y}_{2a}$	s_2^2	n_2	y_{2b}	Pop	Total Pop
Obs. 1													
Jan. 1972	41	476.0	218.7	8	476.0	19,514	21	98	49.2	1	98	2,056	21,570
March 1972	25	523.2	274.6	7	566.4	14,160	190	137	88.1	17	144	27,360	41,520
1908B													
Feb. 1972	11	360.4	35,688.8	6	343.8	3,782	48	95.6	847.8	4	95.6	4,608	8,392
April 1972	18	65.4	1,677.3	7	68.4	1,232	52	7.5	27.4	15	7.7	398	1,630
Obs. 4													
March 1972	21	453.8	34,233.2	6	467.0	9,807	39	111.0	1,481.45	4	111	4,329	14,136
Obs. 4*													
Jan. 1972	9	453.0	48,837.0	5	453.0	4,077	34	133.2	5,181.2	10	126.3	4,294	8,371

* This population was used as another check on the sampling method. The population as estimated by census was 10,104. The error is thus 17.5% of the census estimate.

Note. N_1 and N_2 = number of colonies in the strata of large and small colonies respectively.
y_{1a} and $\bar{y}_{2a}$ = estimate of mean from the initial five samples from large and small colonies.
s_1^2 and s_2^2 = estimate of variance from the initial five samples from large and small colonies.
n_1 and n_2 = estimated number of samples needed for 30% error.
y_{1b} and y_{2b} = final mean estimated from extra samples (chosen at random).
Pop. = population in each of the strata.
Total pop. = number of scale on the tree.

TABLE 8 Sampling data for trees where a large number of scale colonized the leaves.

Tree Number	1842A	Obs. 4	Obs. 1
Number of leaves infested	245	328	1684 *
Mean number of scale/leaf	7.28	8.60	11.29
Number of scale on leaves	1784	2821	19012
% total scale on leaves	40.0	46.2	81.3
Number of scale on twigs	2671	3282	4370
Total population	4455	6103	23382

* The number of leaves infested was estimated as follows:-

The scale were confined mainly to the north-northeast side of the tree, and so the number of leaves this area contained was estimated. Trees grow in an ordered way and to see if it was possible to discover some basic unit with a reasonably constant number of leaves, twelve small secondary branches were chosen at random. All internodal areas and twiglets on the branches were examined and the numbers of leaves growing on each counted. The mean number per secondary branch was 7.77. The number of leaves on the face of the tree was estimated by counting the number of twiglets and internodal areas (623) and multiplying by 7.77. There were therefore 4841 leaves. Of the 667 leaves examined 232 (34.78%) were infested. There were thus 1684 infested leaves on the tree.

TABLE 9 Percentage of female scale surviving.

Tree	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Alverstoke								
Obs. 1	81.2	64.0	48.5	15.9	76.6			
Obs. 2	79.7	26.0	16.1	2.2	72.0			
Obs. 3	71.7	0	-	-	-			
Obs. 4	-	-	11.5	4.9	67.4			
Trees from ant experiment								
A1						0	3.5	-
A4						0	8.3	-
A6						24.9	19.6	-
A8						24.6	7.1	-
A10						40.1	25.8	14.2
A12						-	17.4	56.7
Mean	77.5	30.0	25.4	7.7	72.0	17.9	13.6	35.5
Mallee Block								
1842A	-	0	60.4	64.1	57.7	6.1	15.4	33.3
1821C	-	1.4	0	-	-	-	-	-
1954B	-	-	2.0	25.0	38.2	8.3	2.6	-
1908B	-	-	4.4	37.7	14.9	4.7	5.4	32.0
E. erythronema	-	-	-	-	-	-	-	0
Mean	-	0.7	16.7	42.3	36.9	6.4	7.8	21.8

TABLE 10 Percentage of female scale killed by coccinellids (chiefly *Rhizobius ventralis*)

Tree	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Alverstoke								
Obs. 1	3.1	6.0	0	0	6.1			
Obs. 2	10.4	58.0	1.7	.9	7.5			
Obs. 3	10.9	68.0	-	-	-			
Obs. 4	-	-	2.2	0	13.2			
Trees from ant experiment								
A1						72.2	0	-
A4						97.5	0	-
A6						47.8	0	-
A8						50.8	0	-
A10						40.2	0	45.5
A12						-	0	0
Mean	8.1	44.0	1.3	0.3	8.9	61.7	0	22.8
Mallee Block								
1842A	-	10.5	0	4.3	27.9	53.3	0	0
1821C	-	70.3	0	-	-	-	-	-
1954B	-	-	0	0	23.4	53.0	0	-
1908B	-	-	5.9	7.8	37.3	66.7	0	0
E. erythronema	-	-	-	-	-	-	-	0
Mean	-	40.4	1.5	4.0	29.5	57.7	0	0

TABLE 11 Percentage of female scale killed by hymenoptera.

Tree	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Alverstoke								
Obs. 1	0	2.0	19.4	21.4	2.0			
Obs. 2	0	2.0	8.5	83.6	2.8			
Obs. 3	0	0	-	-	-			
Obs. 4	-	-	12.6	11.0	2.1			
Trees from ant experiment								
A1						14.8	37.9	-
A4						0	79.2	-
A6						1.3	44.7	-
A8						2.1	71.4	-
A10						2.8	49.5	10.4
A12						-	38.0	31.6
Mean	0	1.3	13.5	38.7	2.3	4.2	53.5	21.0
Mallee Block								
1842A	-	2.9	18.9	19.1	.3	3.5	41.5	0
1821C	-	6.4	42.9	-	-	-	-	-
1954B	-	-	56.0	39.3	8.5	8.7	7.8	-
1908B	-	-	27.7	33.8	16.4	6.5	70.5	28.0
E. erythronema	-	-	-	-	-	-	-	21.2
Mean	-	4.7	36.4	30.7	8.4	6.2	39.9	16.4

TABLE 12 Percentage of female scale killed by *Stathmopoda melanochra*.

Tree	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Alverstoke								
Obs. 1	0	4.0	13.0	43.6	2.9			
Obs. 2	0	0	42.4	13.4	0			
Obs. 3	0	0	-	-	-			
Obs. 4	-	-	43.1	76.6	9.3			
Trees from ant experiment								
A1						0	0	-
A4						0	0	-
A6						10.7	3.9	-
A8						2.1	0	-
A10						2.8	0	0
A12						-	0	0
Mean	0	1.3	32.8	44.5	4.1	3.1	0.7	0
Mallee Block								
1842A	-	81.1	0	0	11.4	27.6	0	0
1821C	-	6.4	0	-	-	-	-	-
1954B	-	-	28.0	0	12.8	21.7	0	-
1908B	-	-	51.1	1.3	31.3	13.8	0	0
E. erythronema	-	-	-	-	-	-	-	26.9
Mean	-	43.8	19.8	0.4	18.5	21.0	0	9.0

TABLE 13 Percentage of female scale killed by *Pseudoleucopis beneficia*.

Tree	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Alverstoke								
Obs. 1	3.7	4.0	11.7	4.2	5.6			
Obs. 2	1.8	0.0	28.2	0	14.0			
Obs. 3	0	0.0	-	-	-			
Obs. 4	-	-	23.8	3.4	4.6			
Trees from ant experiment								
A1						7.4	0	-
A4						0	0	-
A6						14.2	1.1	-
A8						7.5	0	-
A10						6.6	0	5.2
A12						-	0	8.5
Mean	1.8	1.3	21.2	2.5	8.1	7.1	0.2	6.9
Mallee Block								
1842A	-	0	0	0	.4	4.5	0	14.3
1821C	-	5.0	0	-	-	-	-	-
1954B	-	-	2.0	7.1	12.8	3.9	0	-
1908B	-	-	.7	6.5	0	4.1	0	0
E. erythronema	-	-	-	-	-	-	-	0
Mean	-	2.5	0.7	4.5	4.4	4.2	0	4.8

TABLE 14 Percentage of female scale killed by causes which could not be identified.

Tree	August 1971	November 1971	January-February 1972	March-April 1972	August 1972	November 1972	January 1973	March 1973
Alverstoke								
Obs. 1	12.0	12.0	7.4	8.4	6.8			
Obs. 2	8.1	4.0	3.1	0	3.7			
Obs. 3	17.4	0	-	-	-			
Obs. 4	-	-	6.8	3.7	3.4			
Trees from ant experiment								
A1						5.6	58.6	-
A4						0	29.9	-
A6						.9	21.4	-
A8						11.9	12.5	-
A10						0	24.7	24.7
A12						-	44.6	3.2
Mean	12.5	5.3	5.8	4.0	4.6	3.7	32.0	14.0
Mallee Block								
1842A	-	5.5	20.8	12.5	2.4	5.0	58.5	52.3
1821C	-	10.5	57.1	-	-	-	-	-
1954B	-	-	2.0	29.6	4.3	4.4	68.8	-
1908B	-	-	10.2	13.0	0	4.2	24.1	40.0
E.erythronema	-	-	-	-	-	-	-	51.9
Mean		8.0	22.5	18.4	2.2	4.5	50.5	48.1

TABLE 15 The number of female nymphs on a small tree and the subsequent number of adult females that settled.

Series I		Series II	
No. female nymphs that moulted to adult	No. adult females that settled	No. female nymphs that moulted to adult	No. adult females that settled
4	4	66	62
8	4	88	77
14	8	88	88
16	16	90	81
36	29	91	83
44	42	165	143
45	44	167	158
53	49	301	94
56	50	310	126
57	55	326	182
113	62	377	28
151	130	380	295
173	112	383	202
260	205	386	187
354	234	525	71
485	98	530	205
600	260	579	148
660	203	653	251
780	730	1476	330

TABLE 16 The relationship between the number of female second instar larvae (cm^{-1} stem and twig length) on the number of adult females settling (cm^{-1} stem and twig length).

Number of female second stage larvae cm^{-1} stem length	Number of adult females settling cm^{-1} stem length
.04	.04
.08	.04
.15	.15
.20	.12
.21	.20
.30	.24
.44	.42
.60	.59
.62	.56
.94	.87
1.54	.84
1.65	1.42
2.28	1.80
2.39	1.55
3.81	3.56
6.10	4.03
6.32	2.74
7.88	1.39
8.57	2.64

TABLE 17(a) The influence of the number of female second instar nymphs on the size of the resulting female scale.

Series I. Kuitpo Forest

Number of second instar female nymphs	Mean size of adult females at reproduction ± 1 standard error mm.
4	2.15 ± .03
8	2.51 ± .18
14	2.38 ± .10
16	2.27 ± .06
36	2.04 ± .07
44	1.92 ± .06
45	2.13 ± .05
57	1.73 ± .05
151	1.76 ± .06
173	1.62 ± .05
260	1.40 ± .03
354	1.39 ± .04
485	1.50 ± .07
600	1.54 ± .03
660	1.42 ± .02
780	1.53 ± .02

TABLE 17(b) The influence of the number of female second instar nymphs on the size of the resulting female scale.

Series II. Kuitpo Forest

Number of second instar female nymphs	Mean size of adult females at reproduction ± 1 standard error
66	2.30 ± .03
88	2.06 ± .03
90	1.78 ± .03
91	1.88 ± .03
167	1.80 ± .04
301	1.72 ± .04
310	1.64 ± .05
326	1.65 ± .04
377	1.44 ± .05
380	1.93 ± .03
383	1.34 ± .02
386	1.91 ± .04
525	1.61 ± .07
530	1.28 ± .03
579	1.62 ± .02
653	1.94 ± .05
1476	1.51 ± .04

TABLE 18 Influence of nymber of female second instar nymphs per cm stem length on the size of resultant females.

Number of female second instar nymphs cm^{-1} stem length	Mean length of resulting females at time of reproduction
.041	2.15
.081	2.51
.145	2.27
.204	2.38
.213	1.92
.296	2.04
.438	1.73
.600	2.13
1.650	1.76
2.281	1.40
2.386	1.62
3.805	1.53
6.103	1.39
6.316	1.54
6.879	1.50
8.571	1.42

TABLE 19 The influence of the number of female second instar nymphs per tree in one generation on the sex ratio of the young in the next generation.

Initial No. female second instar nymphs	Sex ratio (% females) in next generation	No. young examined to determine sex ratio
4	74.2	66
8	83.0	171
14	77.3	88
16	74.1	378
36	63.7	113
44	55.3	398
57	0.0	70
91	45.8	72
167	7.9	240
301	2.4	251
310	31.4	70
380	24.2	462
600	16.9	538
653	15.1	465
660	70.7	123
1476	8.1	236

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