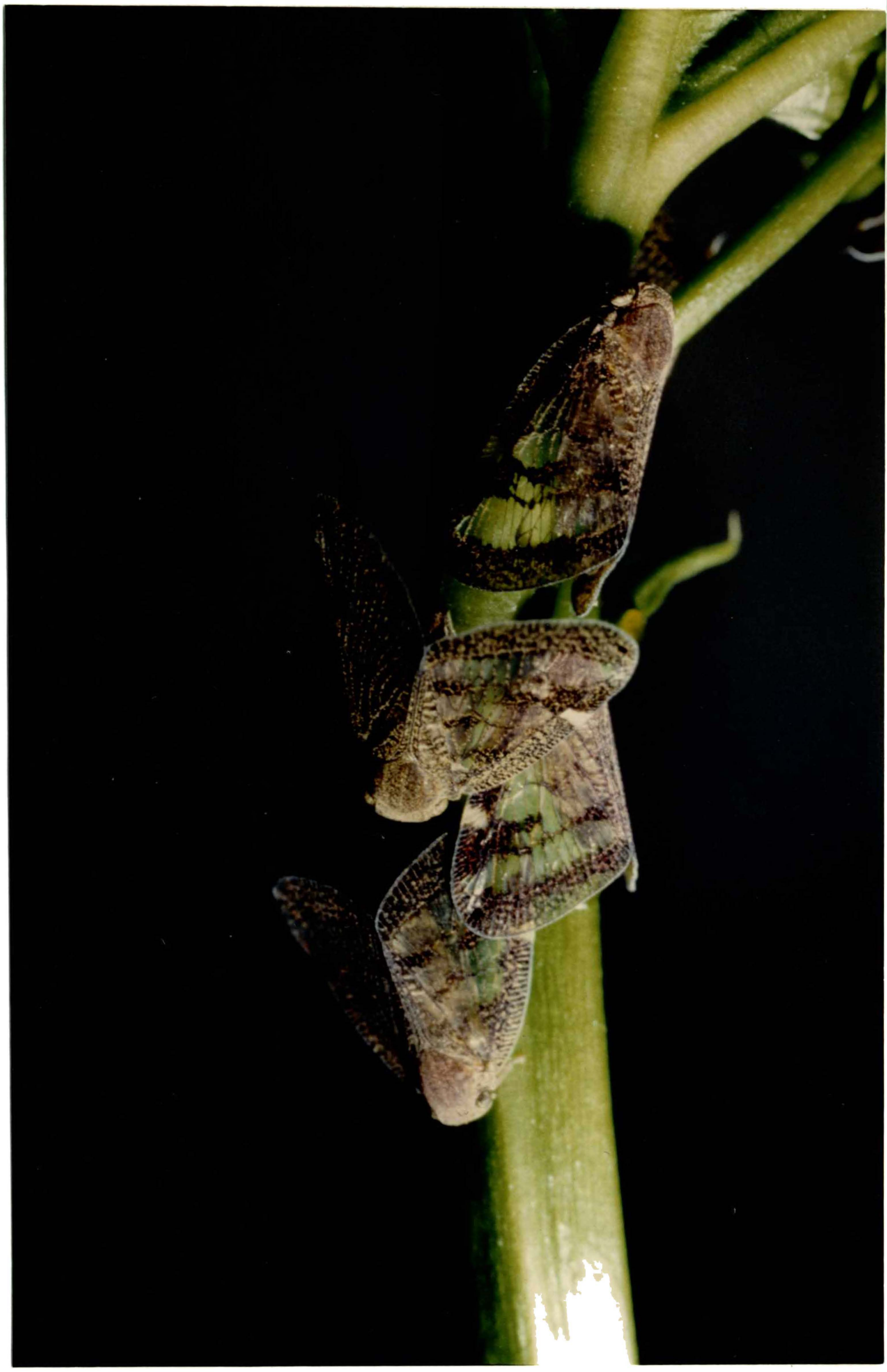

Scolypopa australis adults.

ASPECTS OF THE ECOLOGY OF SCOLYPOPA AUSTRALIS (WALKER) (HOMOPTERA:RICANIIDAE) AND ITS PARASITE CENTRODORA SCOLYPOPAE (VALENTINE)(HYMENOPTERA:APHELINIDAE).

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ABSTRACT

The ecology, population dynamics and interaction, of natural populations of the univoltine passion vine hopper, *Scolypopa australis* Walker, and its egg parasite, *Centrodora scolypopae* Valentine, were studied in a bracken and blackberry filled gully near Hamilton, New Zealand, from 1980-85. The *S. australis* egg population was estimated using a height frequency vegetation sampling method and the nymphal and adult stages by direct counting. The *S. australis* nymphal populations ranged from 200-400/m^2 in the first three generations studied, then fell to below 100/m^2 after a cold summer in 1982-83.

S. australis overwintered as eggs laid mainly in blackberry and bracken stems. Parasitism by *C. scolypopae* was found to be the main cause of egg mortality, followed in importance by fungae, then stem boring insects. Egg mortality varied with height above ground and increased over winter. Host plant had a strong influence on egg survival, mainly because eggs were laid at greater depths in blackberry than in bracken, and thus were less susceptible to parasitism.

Rate of *S. australis* nymphal development differed markedly between years and aspects in response to temperatures experienced. It was slower on blackberry than bracken.

Time specific life table analysis showed that parasitism by *C. scolypopae* was the key factor determining fluctuations in the population of *S. australis*. The next most important factors were variation in natality and adult loss. Neonate loss was the largest cause of mortality and nymphal loss the smallest. No density dependent mortalities were found.

The developmental stages of *C. scolypopae* are described. The larval instars all show a reduction in morphological differentiation when compared with other Aphelinidae. The first instar retains the egg chorion and lacks visible mouthparts, segmentation or tracheae. The third instar has four pairs of spiracles. Adult nutrition, internal and external reproductive systems and mating behaviour are described.

Although *C. scolypopae* females were shown to discriminate between parasitised and nonparasitised host eggs, superparasitism was common in years of high percentage parasitism of host eggs. The progeny of the first oviposition is dominant and eliminates the younger individuals by physiological suppression.

The low temperature threshold for *S. australis* egg eclosion was 10°C and the thermal requirement for completion of the life cycle was estimated between 1500-1900 day degrees. The low temperature threshold for *C. scolypopae* varied with the developmental stage. Egg eclosion required at least 10°C while 14•5°C was needed for the initiation of pupation and adult emergence. *C. scolypopae* was demonstrated to have a facultative diapause in the prepupal stage, that is influenced by both light and temperature.

Life table analysis shows that mortality of overwintering larvae, caused by fungae, twig loss and stem boring insects, was the key factor in the population dynamics of *C. scolypopae*. The 'area of discovery' of *C. scolypopae* was related to both host and searching female density. The mutual interference constant was approximately 1, indicating high levels of interference between searching females. Parasite density was highly dependent on the number of available host eggs. The partial refuge of *S. australis* eggs in blackberry would increase the stability of the host-parasite interaction.

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SECTION A

INTRODUCTION

CHAPTER ONE

GENERAL INTRODUCTION

The passion vine hopper (*Scolypopa australis* Walker) is an insect of pest status that is widely distributed in New Zealand from the North Cape to Nelson. The nymphs and adults feed on an extensive range of native and introduced plants and produce copious quantities of honeydew. Many horticultural crops are attacked, and sooty mould growing on the honeydew disfigures fruit such as kiwi fruit (M.A.F Bulletin 1978), and passion fruit.

Of greatest importance however, is the role of *S. australis* in honey poisoning. When feeding on *Coriaria arborea* (Tutu) the hoppers excrete in their honeydew the plant toxin, tutin, and a less toxic metabolite, hyenanchin (Clinch and Turner 1975). When hot, dry weather during summer dries up normal nectar sources, bees are driven to collect this honeydew. The toxic honey then produced can, in quite small quantities, cause severe reaction in humans. Because of this risk, about 2500 square km of the Bay of Plenty and the whole of the Coromandel Peninsula is closed to beekeeping every summer.

Chemical control of either tutu or *S. australis* to prevent honey poisoning is not feasible because of their extensive distribution. Biological control, which is being investigated by Entomology Division, D.S.I.R. would appear to be the obvious alternative.

The practice of biological control is aimed at restricting the abundance and distribution of target species through the introduction of exotic natural enemies (classical biological control) or manipulation of indigenous natural enemies (Miller 1983). However, although both practices have been successful ecologically and economically (Huffaker and Messenger 1976), the many failures are less well documented. There are controversies concerning the criteria by which exotic natural enemies are selected (Ehler 1976, 1982). Similarly guidelines for selecting species for conservation-augmentation have not been developed. Miller (1983) suggested that the data base for identifying 'ideal' natural enemies is limited and recommended specific studies which could provide insights into the structure of host-parasite communities for the purposes of manipulating indigenous or exotic parasites. In particular, both he and Doutt (1961) recommended the study of native host-parasite interactions. Not only would the 'co-evolved' interaction be similar to that which one might encounter in a search for exotic natural enemies, but such studies are relevant to biological control of the native species.

S. australis eggs are parasitised by the aphelinid *Centrodora scolypopa* Valentine (Hymenoptera:Aphelinidae). This parasite is widespread throughout the Northern North Island causing significant egg mortality in many areas, but according to Cumber (1966) it does not reduce *S. australis* numbers to an acceptable level. The aim of this study was to investigate the interaction between *S. australis* and *C. scolypopae*. As well, this could provide valuable clues on how to manipulate *S. australis* populations and give an insight into the mechanisms involved in the persistence and stability of host parasite interactions.

The study was undertaken with a planned duration of 5 years. Thus it was possible to follow the populations of both host and parasite in the field over a number of generations and by studying the population dynamics of *S. australis*, evaluate the importance of the parasite within the medley of natural mortality factors affecting *S. australis* populations.

The results of the study are presented in two main sections. The first section is on the ecology of a natural *S. australis* population. It looks at the factors determining the abundance of each stage of the life cycle and identifies the key factor responsible for the fluctuations in numbers from generation to generation. The second section is on the biology and ecology of *C. scolypopae*. As well as investigating the interactions with the host and the population dynamics of the parasite itself, it was necessary to collect biological information on *C. scolypopae*. Little is known of the life history or biology of any *Centrodora* species. Most aphelinids are primary parasites of the nymphal stages of sternorrhynchous Homoptera (Aphidoidea, Aleurodoidea and Coccoidea) and so *C. scolypopae* not only provided a fresh area for basic biological study, but also, as an egg parasite, the opportunity to assess any adaptions to this life-style not found in other aphelinidae.

CHAPTER TWO

BACKGROUND INFORMATION ON SCOLYPOPA AUSTRALIS

I SYSTEMATIC POSITION

Scolypopa australis was described first by Walker(1851), as *Pochazia australis* and in 1858 as *Flatoides australis*. Stal(1859) erected the genus *Scolypopa* and *S. australis* was described as a new species, *S. urbana*. In 1862, Stal recognised the synonomy with Walker's species and placed it in the genus *Ricania*. Melichar (1898) replaced it in the genus *Scolypopa* and its current systematic position according to Melichar (1923) is as follows;

Order: Homoptera
Series:Auchenorrhyncha
Superfamily:Fulgoroidea
Family:Ricaniidae
Tribe:Ricaniini
Genus:Scolypopa
Species:australis

There are 6 other known *Scolypopa* species *S. kurandae* (Kirkaldy 1906), *S. scutata* (Stal 1898), *S. stipata* (Walker 1851), *S. delecta* (Melichar 1898), *S. confinis* (Privesa 1906) and *S. aphrophoroides* (Walker 1862).

The common name for *S. australis* is the passion vine hopper even though it has a multitude of plant hosts other than the passion vine (*Passiflora edulis*). This name was first used by Tillyard (1926).

Previously it had been referred to as "tree hopper", "vine hopper" (Kirk 1903) and "passion-vine frog hopper" (Froggatt 1900).

II DISTRIBUTION

Scolypopa australis is a native of Australia where it is found in the coastal regions of Queensland, New South Wales and Victoria. It is also present in Tasmania and the Norfolk and Lord Howe Islands (Mathieson 1978).

It was first recorded in New Zealand by Broun (1876) and in 1896 was recorded attacking grapes and figs in Auckland and Nelson (Thomson 1922). Cumber (1966) surveyed its distribution in New Zealand and found it present from North Cape to Levin in the North Island and in the Blenheim and Nelson areas in the South Island. He found the hopper noticeably absent from higher altitudes and supposed it limited by winter temperatures. Mathieson (1978) noted a close correlation between Cumber's (1966) distribution and the average July 8°C isotherm, the 12°C July daily maximum and the 12°C mean annual temperature isotherm. The hopper distribution may have spread further since Cumber's 1966 survey as *S. australis* has been found in the Taupo area and in moderate numbers in Wellington.

III BIOLOGY OF SCOLYPOPA AUSTRALIS

1 Life history

S. australis has only one generation per year but the developmental stages overlap considerably in New Zealand. October, November and December are the main months of nymphal emergence although eggs may continue to hatch into mid-March (Siew 1960). Adults appear in early January, peak in February and March and may be present till

June in warmer areas (Siew 1960). In colder areas nymphal emergence is delayed and adults disappear earlier (Cumber 1966). Siew (1960) found that adults mate between 10-17 days after moulting and oviposition occurs 1-2 days later. Females then produced further egg batches at 14-16 day intervals and since longevity was 5-7 weeks they could lay at least 3 egg batches.

S. australis overwinters in the egg stage which takes about 6 months in Australia (Fletcher + Anderson 1980) and even longer in New Zealand (Cumber 1966). It was supposed that there was an obligatory diapause (Cumber 1966, Siew 1960, Mathieson 1978) but Fletcher (1980) found that *S. australis* had an exceptionally slow but continous development.

2. Biology and morphology

The external morphology of all stages of *Scolypopa australis* is described in detail by Fletcher (1979) and also by Siew (1960) and Mathieson (1978).

a, Egg

Newly laid *S. australis* eggs are uniformly translucent (Length 770-870 μ, width 360-380 μ). The dorsal surface is slightly more convex than the ventral surface. The chorion is minutely granular with numerous small projections on the anterior third of the surface. There is a funnel shaped micropylar cap at the anterior pole, a vitelline membrane and a further unicellular layer beneath the chorion. Eggs are laid in straight rows into mostly dead twigs, stems, tendrils and petioles of a wide variety of plants. As the ovipositor is withdrawn, plant fibres are drawn out making a distinctive tuft of broken fibres. Oviposition behaviour of *S. australis* is described in detail by Fletcher (1979).

b, Nymphal instars

There are five nymphal instars, all of which have a characteristic fan of waxy filaments held over the body, partly for camouflage and partly to slow descent when hopping (Fletcher 1979). They appear on nymphs before feeding has commenced and are quickly replaced if detached at any time.

The early instars are light brown with dark brown mottling laterally. The body is robust in outline with prominent thorax and small abdomen, usually flexed through 90°-135°. The head and mouthparts are opisthorhynchous with the rostrum reaching to the hind coxae. The 5th instar is brown with white patches particularly laterally on the thorax. The body is very broad across the developing wing pads.

Separation of the instars is readily done by measurement. Fletcher (1979) found the best and easiest characteristics being the length of the body and length of the lateral edge of the mesonotum. Mathieson (1978) found that the comparison of the proboscis length and width of post-clypeus allowed best separation of the nymphal instars.

Adults and nymphs feed mostly on succulent shoots and leaves, often congregating in large numbers. The early nymphs move little but the older nymphs and adults disperse more readily. These are often found on senescing leaves (Siew 1960) possibly because of the higher quantities of soluble compounds available (Yemm 1934).

c, Adult

The adults are brown in coloration and measure 4.8-5.3 mm (males) and 5.9-6.2 (females)(Fletcher 1979). The wings are broad and hyaline with brown veins. The forewings have a brown border, a white patch on the anterior margin and some transverse brown patches in the central portion.

Siew (1960) described the anatomy of the reproductive organs. He found females laid 16-48 eggs per oviposition and that the average dropped in successive ovipositions.

IV PEST STATUS

Scolypopa australis adults and nymphs feed on a very extensive range of host plants. By withdrawing sap from the growing portions of plants, they cause general debility, stunting and wilting (Cumber 1966). Many horticultural crops are attacked. Summer bean crops may be seriously damaged (Toleman pers. comm.). Similarly dahlias, *Lilium*, zinnias and hedge plants such as privet and *Photinia*. Hoppers are one of the major causes of imperfections in kiwifruit (Sale 1983, Ferguson and Stratton 1978, Ferguson 1980, Smith and Graham 1980). *S. australis* has also been recorded as preventing fruit maturation in passion fruit (Cottier 1956), disfiguring passionfruit with sooty mould growing on honeydew (May 1965) and possibly transmitting fireblight (*Erwinia amylovoa*) in orchards (Tillyard 1926). Several insecticides are of some use for control in horticultural crops (Smith and Graham 1980, Ferguson and Stratton 1978). However *S. australis* attacking crops are often spillover from noncrop hosts. Dr C.A. Wearing D.S.I.R., (pers. comm.) suggested any effort to control this pest should be directed principally against the enormous reservoir in waste areas containing species such as bracken and blackberry.

Of most importance, however, may be its role in the production of poisonous honey. High populations of late stage nymphs and adults often occur on *Coriaria arborea* (Tutu) and produce a considerable amount of honeydew. Normally bees are not attracted to the honeydew but during hot, dry weather in summer, normal nectar sources for bees in some areas disappear and bees are driven to collect honeydew (Palmer-Jones et al. 1947).

The Tutu plant produces a toxin (tutin) which is at highest levels in young actively growing parts of Tutu, favoured by the hoppers (Palmer-Jones and White 1949). The hoppers excrete this and a 10 times less toxic metabolite, hyenanchin, in their honeydew (Clinch 1966, Clinch and Turner 1975, Palmer-Jones and White 1949). Honey produced from this toxic honeydew can produce severe reactions in humans, even in quite small quantities. Based on a consumption of 25 g honey at a meal, poisoning would occur at the tutin concentration of 40 mg/kg. Honey samples with this order of tutin equivalents have been found in parts of the North Island. As a result of the discovery of the relationship between bees and *Scolypopa australis* (Palmer-Jones et al. 1947) about 2,500 km^2 of the Bay of Plenty is closed to beekeeping every summer in terms of the Apiaries Act. In 1971 the Apiaries Advisory Committee recommended that the restricted area be enlarged and in 1973 and 1974 the Coromandel Peninsula was also included (Clinch and Turner 1975). Test hives monitoring levels of toxin are maintained by the Apiary Section, Advisory Services Division. M.A.F. in suspect areas throughout New Zealand.

SECTION B

SAMPLING METHODS

CHAPTER THREE

SITE DESCRIPTION

The study area was situated in a gully at Steele's Farm, a New Zealand M.A.F. Insect Control Research area at Rukuhia, near Hamilton and was selected because;

1. The area contained good populations of *Scolypopa australis*.
2. The host plant community was typical of that in which reservoir populations of *S. australis* may dwell in proximity to horticultural crops i.e. as roadsides, gullies, waste areas and beneath shelterbelts.
3. Meterological data would be available from both the Insect Control Group's equipment and the Hamilton Airport which was less than a km. away.
4. Proximity to Hamilton made frequent sampling a feasible proposition.

Within the gully, two sites were selected on opposite sides (Fig 3:1);

Site A; N.E. aspect with gradient averaging 35°.(Plate 3:1)
Site B; S.W. aspect with gradient averaging 30°.(Plate 3:2)

Paths were cut down vertically at each end of the sites and permanent steps installed because of the unstable nature of the light, sandy soil. Between these steps, 2 roughly parallel paths were cut, one at the upper level of the gully, the other at the lower level. The horizontal paths were more open in places than the vertical paths because of the nature of the vegetation. Where the gradient was steepest the vegetation fell away when cut. Once the paths were in place, the vegetation was disturbed as little as possible. Each of the

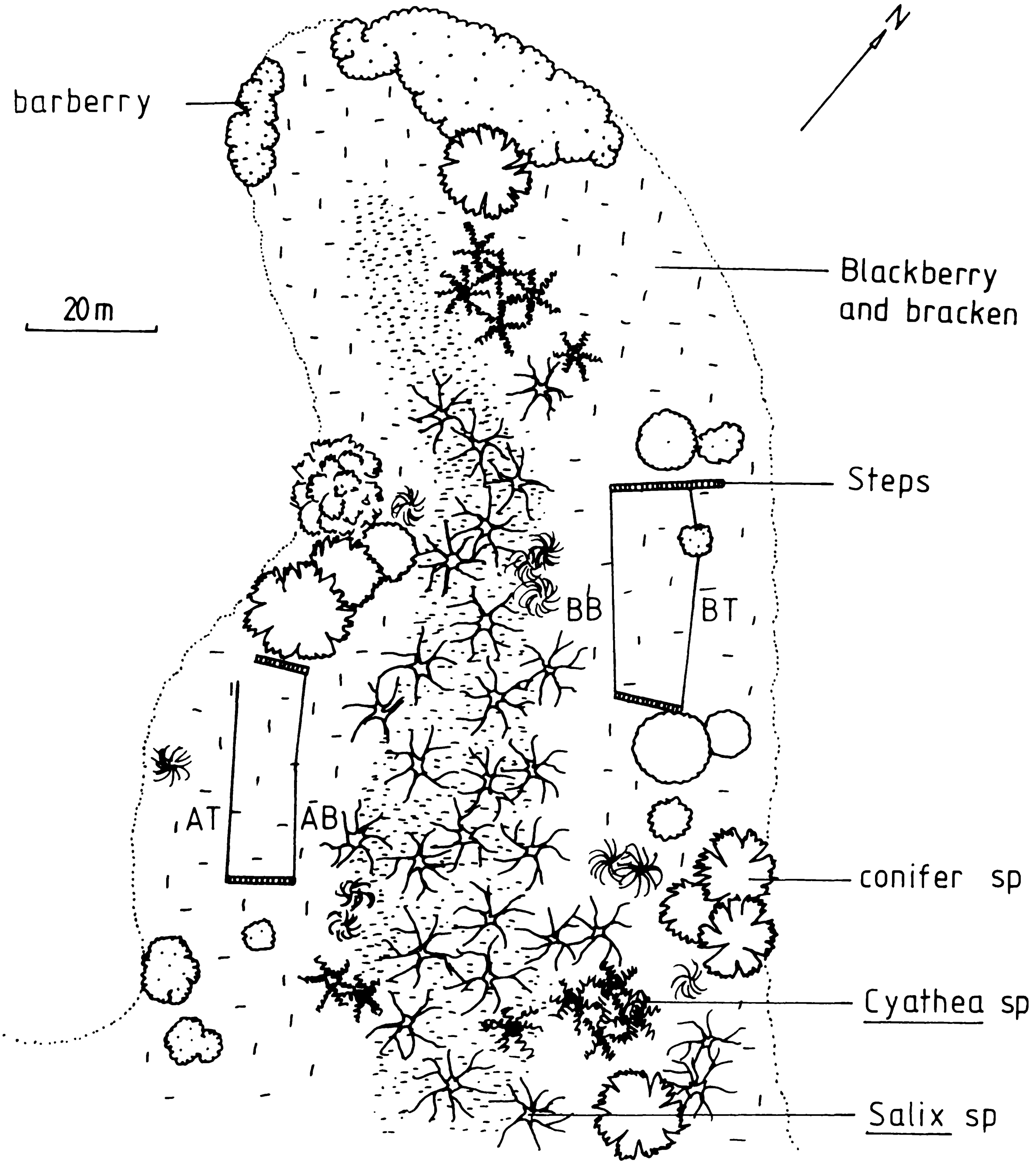

Fig 3:1 Position of Blocks AT, AB, BT and BB within gully at Steele's Farm, Rukuhia.

4 horizontal paths represented a sampling block. Those on Site A were called AT (top) and AB (bottom) and similarly on Site B, BT and BB. (Fig 3:1). They varied in length as obstacles such as tree stumps, and deep hollows had to be circumvented, preventing a straight line being cut. Although path BT measured 30 m, the actual length sampled was 25 m. This was because BT passed through a small cluster of barberry (*Berberis darwinii*), and *Coprosma robusta* and since not typical of the site as a whole, a distance of 5m encompassing these trees was excluded.

The composition of the vegetation in all blocks was assessed in October 1980 by a height frequency method described by Scott (1965). The results are summarised in Fig 3:2. Bracken (*Pteridium aquilinum* var. *esculentum*) was the most dominant species in all blocks followed by blackberry (*Rubus fruticosus* agg.). Black bindweed (*Polygonum convolvulus*) was moderately abundant on the S.W. aspect. The only other species of any frequency were barberry, sweet briar (*Rosa rubiginosa*), Mahoe (*Melicytus ramiflorus*), *Convolvulus anensis*, *Coprosma robusta* and *Hebe stricta*.

The amount of bracken and blackberry did not change over the period of the study as can be seen by comparison of a subsequent vegetation sampling in 1984 (Fig 3:3) with Fig 3:2. There was a decrease in the other species present, some of which was due to removal of barberry and sweet briar which were unpleasant to work alongside. After the bracken had reached maturity, the vegetation subsided with the weight of the new growth. Thus the height at which the maximum frequency of any vegetation component occurred was lower after winter than in autumn (compare Fig 3:2 and Fig 3:3). For sampling purposes, bracken and blackberry were divided into new (growth from the previous spring and summer) and old (dead material from previous years) categories.

Plate 3:1 Site A, Steele's Farm, Rukuhia, Spring 1984.

Plate 3:2 Site B, Steele's Farm, Rukuhia, Spring 1984.

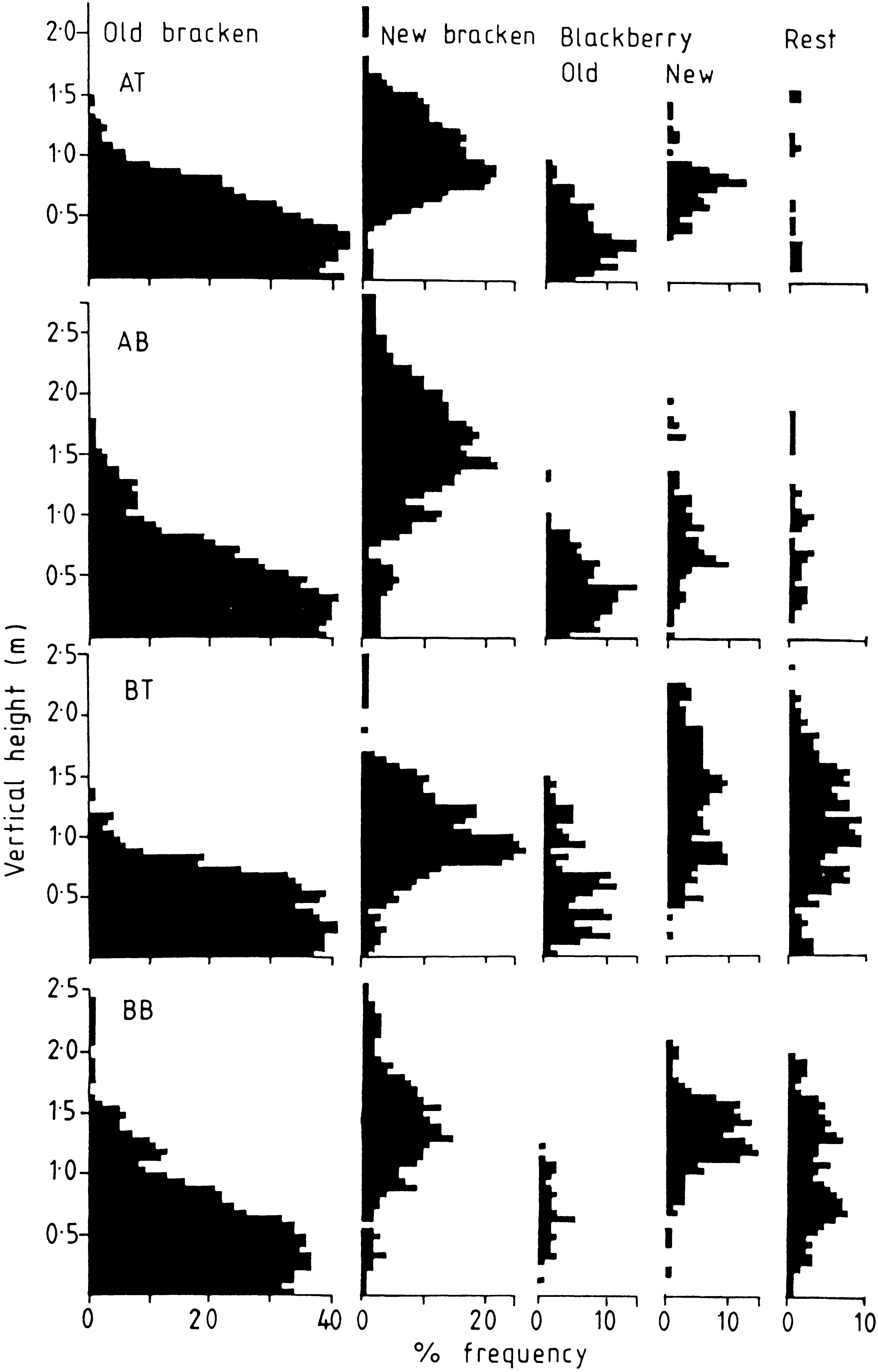

Fig 3:2 Height frequency diagram of vegetation in each block (AT, AB, BT and BB) in gully, Steele's Farm, October 1980.

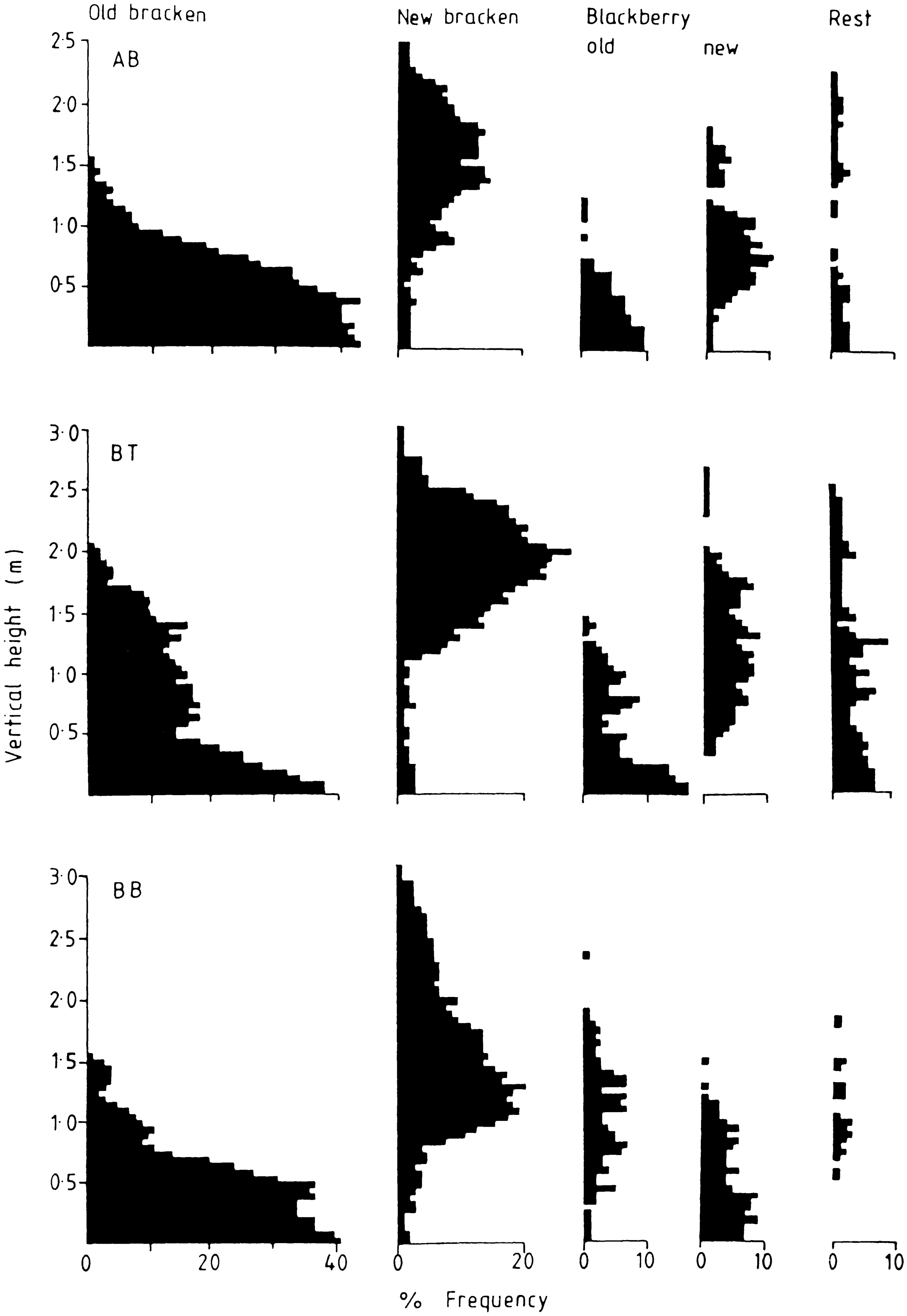

Fig 3:3 Height frequency diagram of vegetation in each block (AB, BT and BB) in gully, Steele's Farm, May-June 1984.

CHAPTER FOUR

SAMPLING TECHNIQUES

I INTRODUCTION

Southwood (1966) stated that vegetation is in many ways the most difficult habitat to sample insects from: it differs from soil and the air in being much more heterogeneous and in continually changing. The interwoven bracken and blackberry on the steeply sloping study area exemplify these problems (Plates 4:1 and 4:2). Not only was an absolute estimate of the egg population needed but also the distribution between the plant species present. Similarly, obtaining a good estimate of *Scolypopa australis* nymphal and adult populations was difficult.

The main host plants ranged in height from ground level to over 3.5 m. Bracken has underground stems with fine fibrous roots. These branch in a complex manner and penetrate deep into the soil. Rhizomes near the surface give rise to several new fronds each year. On the site, frond production begins during October. The majority of fronds appear simultaneously with only a few relatively weak fronds appearing during the summer. Thick fleshy shoots grow 1-2 m before the fronds begin to unfurl. Such a profusion is produced that a canopy of fern is formed. The weight of mature fronds causes the bracken to fall forming a dense layer as time passes. Fronds usually persist only for one year and the following season's fronds grow up through the previous season's growth.

Blackberry is a woody perennial. During spring, strong fleshy shoots appear. Side branches quickly form and the blackberry climbs

Plate 4:1 View of Block AB, Spring 1984.

Plate 4:2 View down steps at right of Site B, Spring 1984.

through, over and above the bracken profusion and a tangled, thorny thicket is formed. The production of fleshy vegetative shoots ceases when flowers appear and fruit forms but further growth does occur in late summer especially if there is plentiful rainfall.

II EGG AND VEGETATION SAMPLING

Scolypopa australis laid eggs on all plants in the trial area and the eggs were inserted into woody tissue in longitudinal rows. During 1980, while the paths were being cut into the vegetation, an attempt was made to sample the egg population by cutting all plant material within a 0.5 m^2 quadrat and sorting through it for egg batches. This was extremely slow (1 sample/hour) and because so few samples were processed, gave large errors in estimates. Also it was a destructive method of sampling, and it was clear that if widely used, it would alter the composition of the trial area.

A modification of Scott's (1965) height frequency sampling method, was thus tried and proved to be extremely suitable. The principle of the method involves the measurement of plant and egg frequency in successive layers within the vegetation. The layers are parallel with the ground and frequency in each layer is determined by noting the presence or absence of a species and the respective number of egg batches in small volumes within this layer. For convenience, the sample volumes for successive layers are taken one above each other, thus becoming segments of a vertical sampling column. In practice, this involved using a rod 2 m long, pierced with holes at 5 cm intervals. A volume of 5 cm^3 was defined by a U shaped piece of metal consisting of a solid back with a protruding screw in the centre, and two 'fingers' top and bottom for the sides. The screw slotted into the holes on the rod. (Fig 4:1).

The advantages of this method were that it provided an absolute estimate of the egg batch population, and also the distribution between host plants and within the plant canopy. The method was relatively nondestructive, the vegetation being damaged only when it was so thick that some had to be cut to see what was within the sampling unit. The field time for a single operator was approximately 20 samples per hour when both plant and egg frequency was recorded or 50 per hour when only egg frequency was taken.

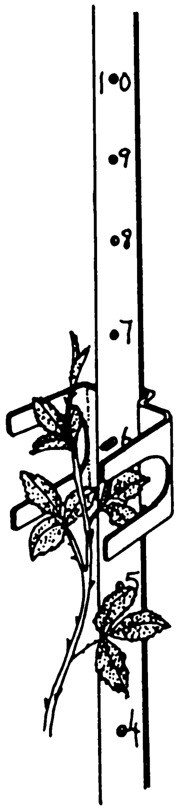

Fig 4:1 Diagram of sampling apparatus.

At each site, five 2x1 m plots were marked, at random along each of the 4 paths and approximately 30 cm into the vegetation from the paths (20 plots in all). As vegetation could be sampled from either side of the path, the length of vegetation available for sampling was twice the lengths of the paths. It is acknowledged that there would be an 'edge' effect from the paths but the nature of vegetation and site made this effect very difficult to eliminate.

Within each plot, the sampling points were selected at random. The rod was lowered vertically through the vegetation till it touched the ground. The heights at which various species intercepted the column and the number of egg batches on each were recorded. An egg batch had to be at least half in the volumetric measure to be counted and eggs laid singly were ignored. This method gave a standard error, for mean study area egg density, of 8-12% of the mean in the first three generations and around 15% when populations fell to low levels in 1983 and 1984 (Appendix 2).

The first population sampling with Scott's method was undertaken at the end of October and early November 1980. It was then repeated yearly both just after *Scolypopa* oviposition had ceased (May-June) and just prior to nymphal emergence (October-November) to give pre- and post-winter estimates. Egg estimates only were made in October 1983 and 1984. Ten samples were taken in each plot except in 1981 when 14 were taken in AT plots, 16 from BT plots and 12 from BB plots.

Block AT had to be excluded from population estimates from late 1983 after cattle invaded the trial site and demolished the top half of site A. Regeneration of vegetation was very slow because of the sandy soil which slipped away under the cattle's hooves resulting in destruction of underground roots and rhizomes.

III NYMPH AND ADULT POPULATION SAMPLING

Previous workers on leafhopper populations have monitored adult and nymphal numbers using numerous techniques. Light traps (Otake 1978), sticky traps (Waloff 1980, Williams 1984) and aerial suction traps (Waloff and Thompson 1980) have provided relative estimates of population. Sweepnet (Waloff and Thompson 1980) and vaccuum suction methods (Waloff 1980) have been used for grassland leafhoppers and leaf sampling for those on blackberry (Williams 1984). Sweeping was not considered as blackberry has many thorns and suction methods would not have worked well with the large, robust hoppers. Sticky traps were dismissed as would give a purely qualitative assessment.

The *Scolypopa australis* population is highly aggregated, especially the early instars which can be found clustered on the top 20cm of bracken shoots or along the length of succulent blackberry shoots. Until the fourth instar the nymphs do not disperse readily unless disturbed. Because of these attributes and because the population is not a 'closed' one, nearest neighbour and capture-recapture methods of population estimation were not considered appropriate and direct counting was selected as the most feasible method especially since *Scolypopa* individuals are moderately conspicuous. This method was used by Materu (1971) in population dynamic studies on *Acanthomia* spp. (Hemiptera : Coreidae) and also by Stiling (1980).

Counting of early instars was relatively simple and quick, especially in spring before the bracken unfurled (Plate 4:1) and the blackberry started to branch. Each spring, five 2x1 m plots were marked out alongside each path. These plots were retained for all nymph, adult and egg samplings until the following spring. The upright bracken stems could be pulled into view without disturbing the hoppers. It was found that instars could be differentiated by size quite readily and each instar was counted separately and recorded. Initially reference samples that had previously been sorted in the laboratory using Fletcher's (1979) characteristics, were taken into the field to assist instar separation but this precaution was soon dispensed with.

By mid-January, the bracken was beginning to become entangled. However the hoppers at this stage were 5th instars or adults and readily visible, so not impossible to count. Once counted, the frond was sometimes untangled from its neighbours, especially if it had fallen downhill at right angles to the path, so it would be in a more accessible position at the next sampling.

Populations on blackberry were sampled on succulent growing shoots by counting the number of each instar on the shoot and undersurface of leaves back to and including the 3rd fully expanded leaf. Flowering blackberry shoots were not sampled as very few hoppers fed on these. (Blackberry was not included in any population estimates after the initial sampling in the 1982-83 season only. At this time it became apparent that it was desirable to conduct more frequent samplings than had been taken in the previous two years so that hopper development could be followed. However field operations had to be unavoidably restricted to about 3.5 hours on a Sunday,[1] so blackberry was omitted for the remainder of the 1982-83 season as being too difficult and time consuming to sample).

The number of bracken fronds and blackberry shoots were estimated by laying 1 m quadrats on the vegetation and counting the number of bracken stems arising and blackberry tips terminating within each quadrat. Almost all bracken stems arise during spring and any subsequent ones are few in number and very small, usually less than 1 m high. By midsummer, bracken stem numbers are constant and a sampling then suffices for any subsequent population estimates.

As the development, as well as the density of the population, was being assessed, it was desirable that each sampling was completed

---

[1] New baby!

within the space of a day or two. Therefore a compromise had to be made between the degree of precision and the number of samples one person could achieve. Morris (1955) suggested that the sampling plan should be designed so that the standard error was 10% of the sample mean. Since then, the proposal has been widely used although life tables have been constructed where the percentage standard error has been greater than 20% relative standard error (King 1979). It was found that 5 stems per plot (25 bracken and blackberry stems per block) was the maximum that could be sampled in the time available and although the error was over 10% of the sample mean, it was almost always below 20% for block estimates.

This sampling method underestimates the total population in the area and as such should be regarded as a relative rather than absolute sample of the population. Parts of the blackberry remain unsampled and other plant species are ignored. However, observation of hopper distribution amongst the vegetation during the 5 years of this study would suggest that over 90% of the population would be on the parts of these two species sampled and near 100% at the initial sampling when hoppers have no alternative food source.

IV EGG MORTALITY

1980

Egg mortality estimates were obtained by examining eggs from batches collected at the time of the population sampling. Each oviposition scar was twisted so that it split along the scar and enabled the eggs to be spilt out into a petri dish. The eggs were then separated into groups of normal, parasitised, fungal infected, and any other cause of mortality. Estimates of mortality were then expressed as percentages for each sample bag. This method did not give any estimates of mortality factors which leave no remains such as twig breakage.

1981

Blackberry and bracken twigs bearing oviposition scars were collected during May then again in October for pre- and post-winter estimates of egg mortality. The vegetation on each of the 4 blocks was divided visually into 3 layers;

a, Upper canopy : predominantly current season's growth. This was relatively open compared with the lower levels.

b, Middle zone : mainly densely packed dead growth from last season.

c, Lower zone : All vegetation within about 30cm above ground level. Much of this was visibly decayed.

Twigs bearing oviposition scars were collected along the full length of each site and put into labelled plastic bags. These were stored at 4°C and examined as soon as possible to avoid desiccation. A twig would be picked out of the sample bag and placed under the microscope. The first oviposition scar viewed was then cut with a scalpel to expose a dorsolateral view of the eggs within the woody tissue. The number of eggs laid was recorded, then the numbers surviving, diseased, shrivelled, eaten, parasitised or killed any other way. The procedure was repeated until 20 oviposition scars from both bracken and blackberry from each sample bag had been processed, giving a total of 120 batches per block.

1982-1984

On each of the 4 blocks, five 2x1 m plots had been sampled for egg density soon after the last adults had disappeared. For a pre-winter estimate of egg mortality, twigs bearing oviposition scars were collected from the middle zone vegetation immediately adjacent to each of these plots. They were not collected from within the plots as a further population sampling was to be undertaken just prior to nymphal emergence. Once this second egg population sampling had been completed, further oviposition material was gathered from within the plots to estimate final egg survival over winter. In the laboratory the eggs were examined for mortality as described above, except that only 10 oviposition scars from each plant species were examined per plot, a total of 100 batches per block.

V COLLECTION AND ANALYSIS OF TEMPERATURE DATA.

Daily temperatures were recorded in Blocks AT and BT with the use of 'Belfort' monthly cycle recorders. These were placed in covered stands erected adjacent to the vertical paths within the plant canopy where *S. australis* nymphs and eggs were most dense. As temperatures were not recorded in the gully during the first two years, the maximum and minimum daily temperatures recorded at Rukuhia Airport from 1980-85 were obtained from the N.Z. Meteorological Service to allow comparison between years.

Thermal summation, in the form of day-degrees, often predicts insect development more satisfactorily than chronological time (Riedl et al 1976, AliNiazee 1979, Whalon and Smilowitz 1979). The day-degree summations at both the trial area and Rukuhia Airport were calculated using a Fortran 77 computer programme obtained from S. Worner, Lincoln College, using the model of Baskerville and Emin (1969). This model was found by Worner and Penman (1983) to predict temperature profiles approximating sine waves, such as found in Hamilton, more accurately than models of Parton and Logan (1981) and the Blunck-Bodenheiner formula (Arnold 1960).

SECTION C

SCOLYPOPA AUSTRALIS POPULATION ECOLOGY

CHAPTER FIVE

EGG POPULATIONS

Absolute estimates of the numbers and sizes of *S. australis* egg batches were obtained from 1980 to 1984 (Appendix 1). In the first two years, only one population sampling per year was undertaken, (October 1980 and June 1981) but as egg numbers were seen to decline over winter, in subsequent years the egg population was sampled twice, immediately after oviposition (May-June) and just prior or during hatching (October- November).

I EGG DISTRIBUTION WITHIN VEGETATION

The vertical distribution of blackberry, bracken and other plant species and the corresponding egg batch distribution for the combined May-June samplings in the study area is presented in Fig 5:1. The results for the October-November samplings are shown in Fig 5:2.

S. australis lay their eggs predominantly in sheltered and dried out woody twigs and stems. This provides protection from direct sunlight, excessive moisture and weather extremes. Green live plant tissue is largely avoided but when population pressure is high indiscriminate oviposition occurs. Eggs laid in green stems are vulnerable to damage when the stems twist and shrivel as they dry (Cumber 1966). Figs 5:1 and 5:2 show the preferences of ovipositing females. The current season's bracken, which forms the upper canopy, was not used for oviposition and visibly decaying material near ground level, which is often wet for prolonged periods, was also avoided. Cumber (1966) also noted that egg survival was poor on low growing

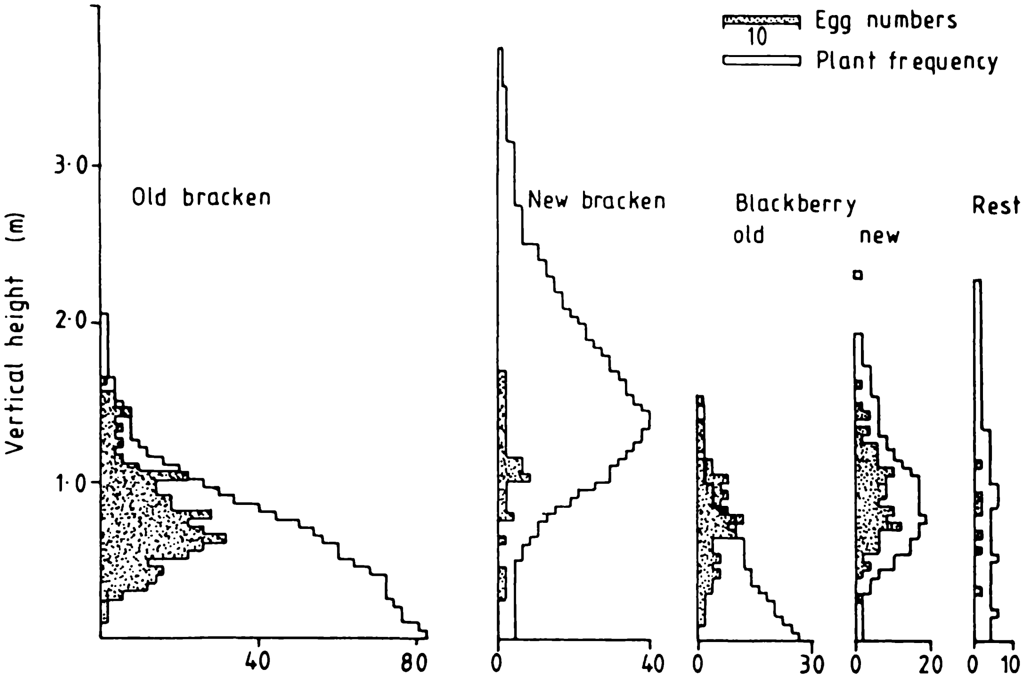

Fig 5:1 Combined block and year height frequency histogram of vegetation and *S. australis* egg batches at June, 1981-84.

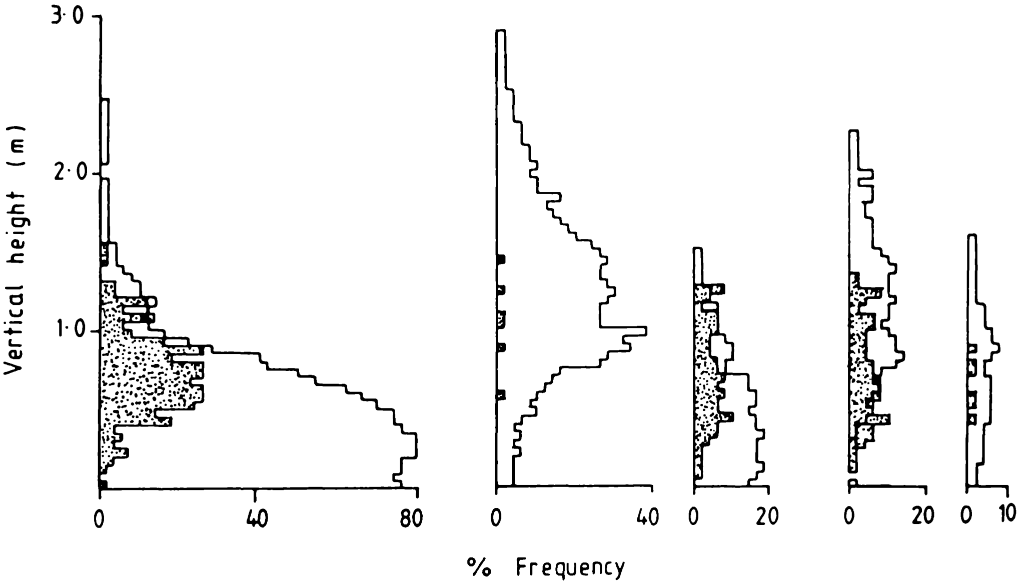

Fig 5:2 Combined block and year height frequency histogram of vegetation and *S. australis* egg batches at October, 1980-83. (Key as in Fig 5:1)

stems. Consequently the majority of eggs are laid from 0.75-1.25 m above ground level.

Current season's and old blackberry appear to be equally favoured for oviposition (Fig 5:1). However the majority of eggs laid on new blackberry are found in the petioles of senescing and dead leaves. These petioles are not as stable as dead twigs and stems, and many drop to the ground and disappear during the winter months, accounting for much of the observed decrease in egg batch numbers in new blackberry at the spring sampling.

Even though there is less old blackberry than old bracken in the study area (Figs 5:1,2), the ratio of eggs to plant frequency when compared at 5 cm height intervals is significantly greater for blackberry (t=3•185 P<•01), indicating that old blackberry is preferred to old bracken as an oviposition material. This was tested experimentally. Twelve stems of dead bracken were paired with stems of dead blackberry, according to stem diameter, which ranged from 2-8 mm. Each pair was attached to a folded cardboard strip so that they were parallel, about 2 cm apart, and 10 cm of each stem exposed. All 12 pairs were placed in a jasmine vine (*Jasminum polyanthum*) heavily infested with *S. australis* in the author's Hamilton garden. Several weeks later the pairs were inspected for oviposition. Although there was wide variation between stems, bracken was less preferred averaging 11•42±3•28 (range 0-37) batches/stem while blackberry averaged 18•75±3•38 (range 2-38). More obvious was the difference in the number of eggs laid. Bracken averaged only 4•82±•37 eggs per batch while blackberry averaged 9•88±•43 (t=8•135 P<•001). *Scolypopa australis* females presumably prefer to oviposit in blackberry as it has a soft pithy interior in the stems which would enable easier oviposition than the hard bracken stems.

II EGG BATCH DENSITY

The mean density of egg batches in both bracken and blackberry in the study area from 1980 to 1984 inclusive are presented in Fig 5:3. *S. australis* egg batch numbers fluctuated over the years with 1980 and 1982 having highest numbers and 1981, 1983 and particularly 1984 showing low batch numbers.

The distribution of batch numbers was not even over the study site and varied with the years as can be seen from Fig 5:4. In 1980, very high numbers were found in BB with moderate numbers in all other blocks. The following year, all but AB showed a decrease in numbers, particularly BB after the high levels of the previous year. The large increase in 1982 was concentrated in the lower blocks, AB and BB and these two showed marked decreases in the following year. The numbers remained low throughout the area in 1984.

The distribution within the study area could be partly caused by the ovipositing females responding to temperature and humidity. Block AT is exposed to the sun for the longest time each day and AB and BB in the lower portion of the gully are more sheltered and probably more humid. Both 1981 and 1982 were relatively warm summers. From mid January to mid March, the main oviposition period, they totaled 549 and 499 day degrees respectively. In contrast, 1983 was a cold year and only accumulated 401 day degrees over the same time period. When Fig 5:3 and 5:4 are compared it can be seen that block AT does not show the same increase in numbers in 1982 that the area as a whole exhibited. It is possible that fecund females moved away from this exposed area into the more favourable gully blocks. The following year when temperatures were low, instead of showing the marked decline in numbers of the other blocks, AT showed a small, although statistically

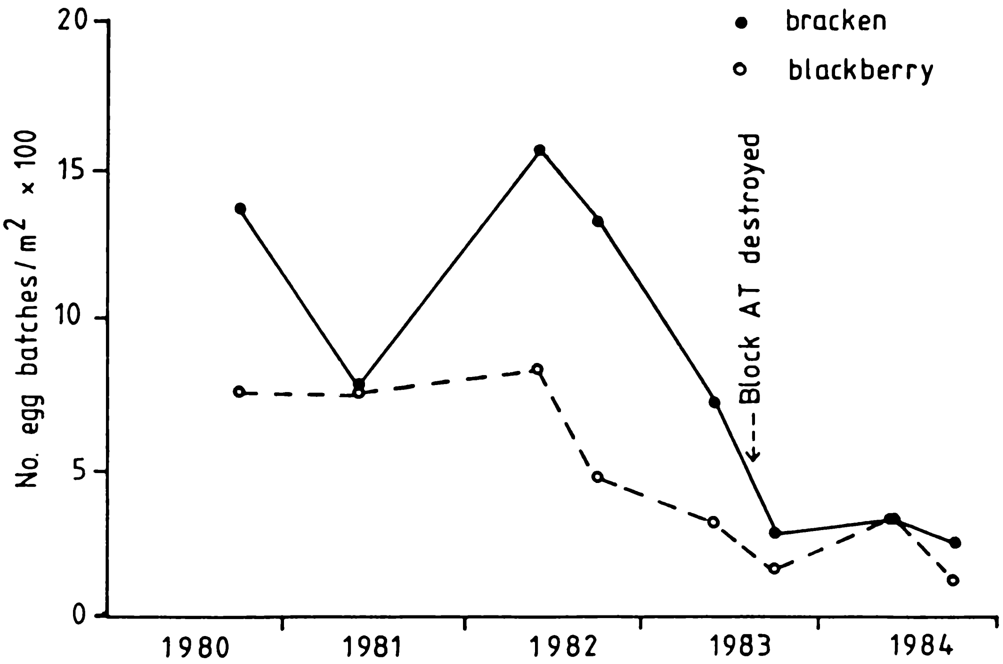

Fig 5:3 Number of *S. australis* egg batches per m^2 in blackberry and bracken, Steele's Farm gully, 1980-84.

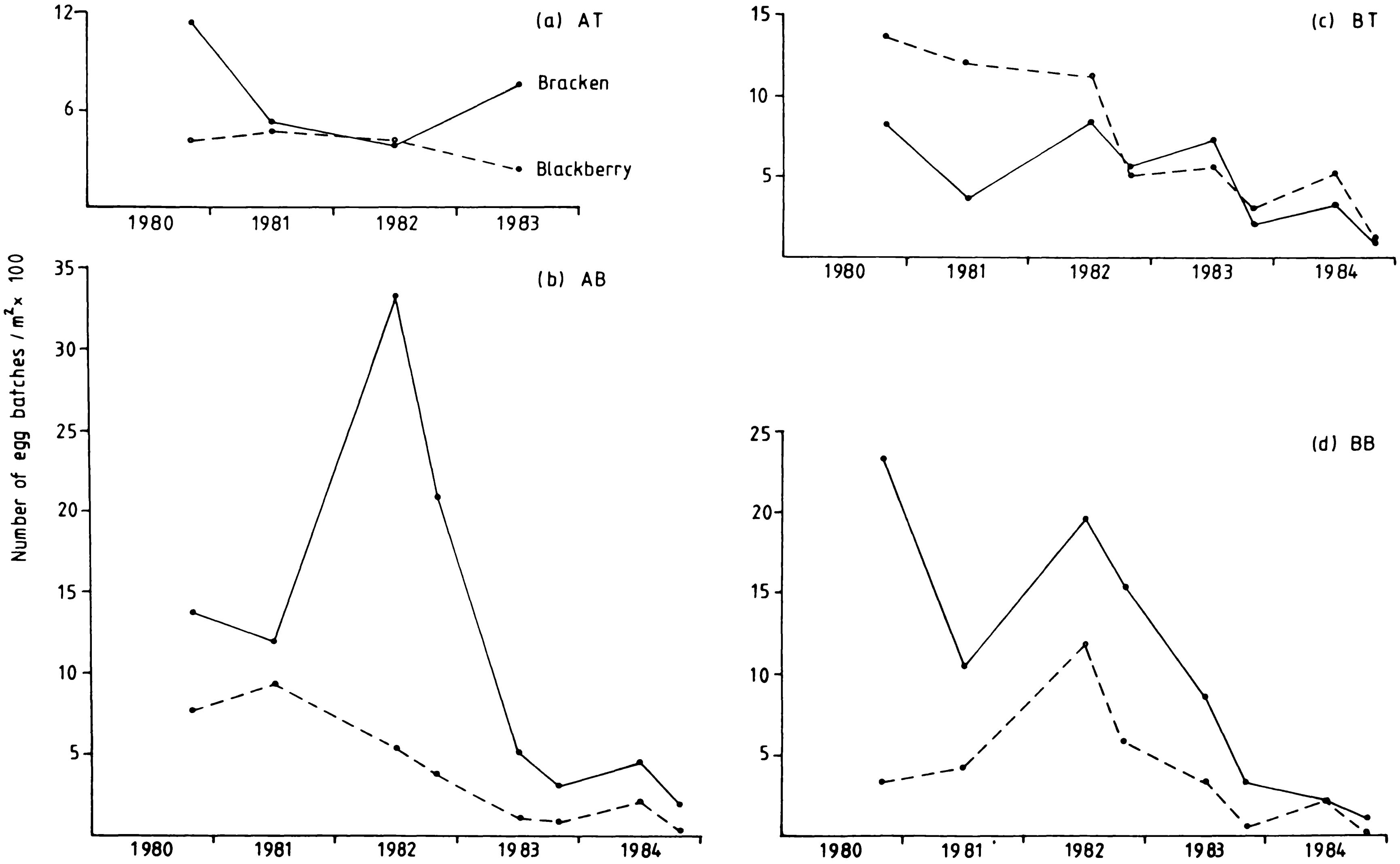

Fig 5:4 Mean number of egg batches / m^2 in each block in gully, Steele's Farm; 1980-84.

insignificant, increase. The additional exposure to the sun this year may have made AT a relatively more favourable area.

It is noticable that when populations were high in BB in 1980 and in AB in 1982, a far higher proportion of the eggs were on bracken than on blackberry compared to other years. Possibly females oviposit more readily on the less preferred but more abundant bracken when population pressure is high, rather than spend longer searching for blackberry.

S. australis females have a fecundity of between 28-48 eggs at the time of their first oviposition (Siew 1960) and may produce 2 subsequent egg complements. However females do not generally lay all their eggs as a single batch. Fig 5:5 presents histograms of egg batch sizes laid in the study area in 1980. Batch size on bracken averaged 6.50±•11 and on blackberry 8•22±•18. Even though blackberry twigs are liberally scattered with thorns which interupt egg batches, egg batch sizes are still large indicating the preference of the ovipositing females.

III EGG POPULATION

The egg population was established by multiplying the mean number of egg batches by the mean size of egg batch for each block, separately for both bracken and blackberry. The results are presented in Fig 5:6 and Appendix 2. Egg density closely follows the distribution of egg batches (Fig 5:3), except that the proportion of the population on blackberry has increased because of the larger average egg batch sizes on blackberry.

Finally, the number of live *S. australis* eggs/m^2, obtained by assessing the proportion of eggs surviving in each block is presented in Fig 5:7 and Appendix 2. Assumptions are made, in particular that the distribution was described by a binomial distribution. This is not strictly correct as some mortality factors, particularly fungal incidence and the destruction of eggs by wood boring larvae, are clustered. Bearing in mind these reservations, Fig 5:7 still shows significant population trends: the 1981 decline in population is no longer apparent. Large egg mortalities occurred in the winter of 1982 and by the end of winter 1983, numbers were exceedingly low. The importance of blackberry to the overall population is demonstrated by it becoming the main contributor to the surviving population in Fig 5:7 as compared with initial egg batch distribution in Fig 5:3.

```
a,                Bracken
   Batch size
       1-2        **************************
        -4        **************************************
        -6        **********************************
        -8        ***************************
       -10        ***************
       -12        ***********
       -14        ******
       -16        *****
       -18        ****
       -20        **
       -22        *
       -24        *
       -26        *
       -28        *

       N = 1671   Each * represents 10 observations.


b,                Blackberry
   Batch size
       1-2        ************
        -4        *****************************
        -6        ******************************
        -8        *****************************
       -10        **********************
       -12        **************
       -14        ***********
       -16        ******
       -18        *****
       -20        ***
       -22        **
       -24        *
       -26        *
       -28        *
       -30        *

       N = 811    Each * represents 5 observations.
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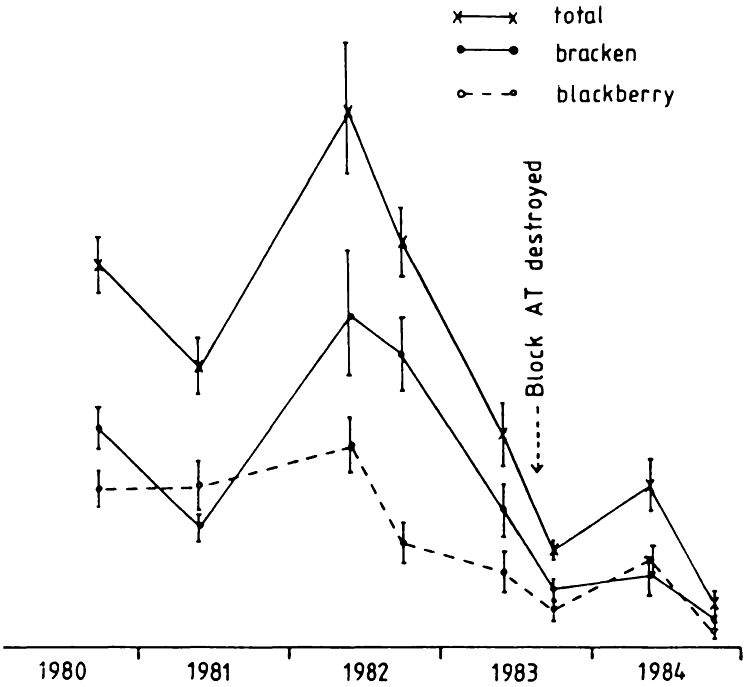
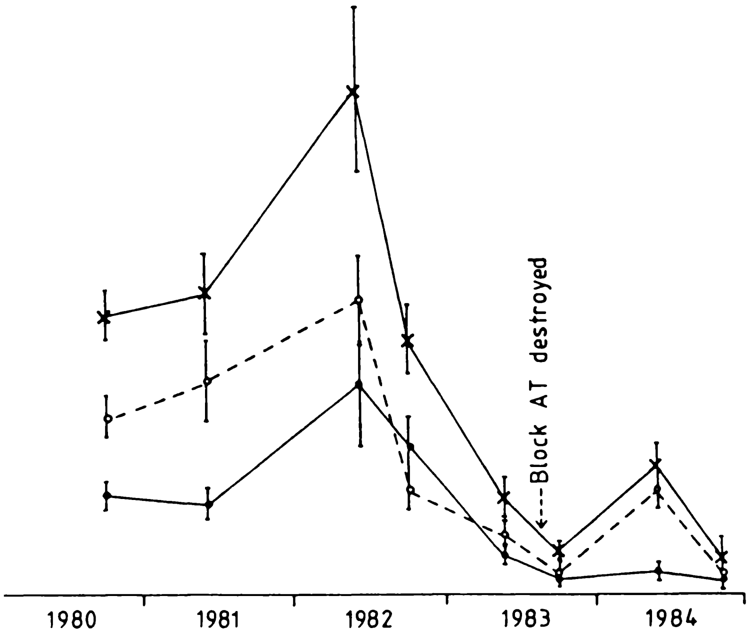
Fig 5:5 Histograms of *S. australis* egg batch size in Steele's Farm Gully 1980.



Number of *S. australis* eggs per m^2 in Steele's Farm ully, 1980-84.



Number of surviving *S. australis* eggs per m^2 in teele's Farm gully, 1980-84. (Key as for Fig 5:6).

CHAPTER SIX

EGG MORTALITY

Scolypopa australis overwinters as the egg stage which is present in the egg site from mid January, when oviposition begins, till October when nymphal emergence commences. The long duration of the stage gives ample opportunity for a range of mortality factors to act and cause substantial losses. Cumber (1964, 1966) surveyed over 100 sites throughout the range of *S. australis* in New Zealand in late winter 1962. In the central North Island, he found an average 46% of eggs survived, 23% were parasitised by *Centrodora scolypopae*, 22% shrivelled from various causes, 3% were destroyed by tunnelling larvae and less than 1% were infertile. In Australia, Cumber (1967) found *S. australis* eggs were parasitised by *C. scolypopae* and an unidentified scelionid species and were attacked by a chrysopid predator. However survival was higher than in New Zealand with 61-67% of eggs hatching in the Sydney area.

Egg survival and the main categories of egg mortality of the *S. australis* population over the study period are presented in Appendices 3-12 and are summarised in Fig 6:1. No allowance has been made for egg batch loss caused by the breaking and disappearance of twigs, stems and petioles. At the time of sampling in 1980, the trial area had been divided only in half and thus the blocks for each half are given identical values. For the 1981 egg mortality assessments, when eggs were sampled from 3 heights, only the values for the middle height are used in Fig 6:1, since most of the population occurs at that level. The results of these 1981 assessments showing the influence of position within the vegetation on egg survival and several mortality factors are

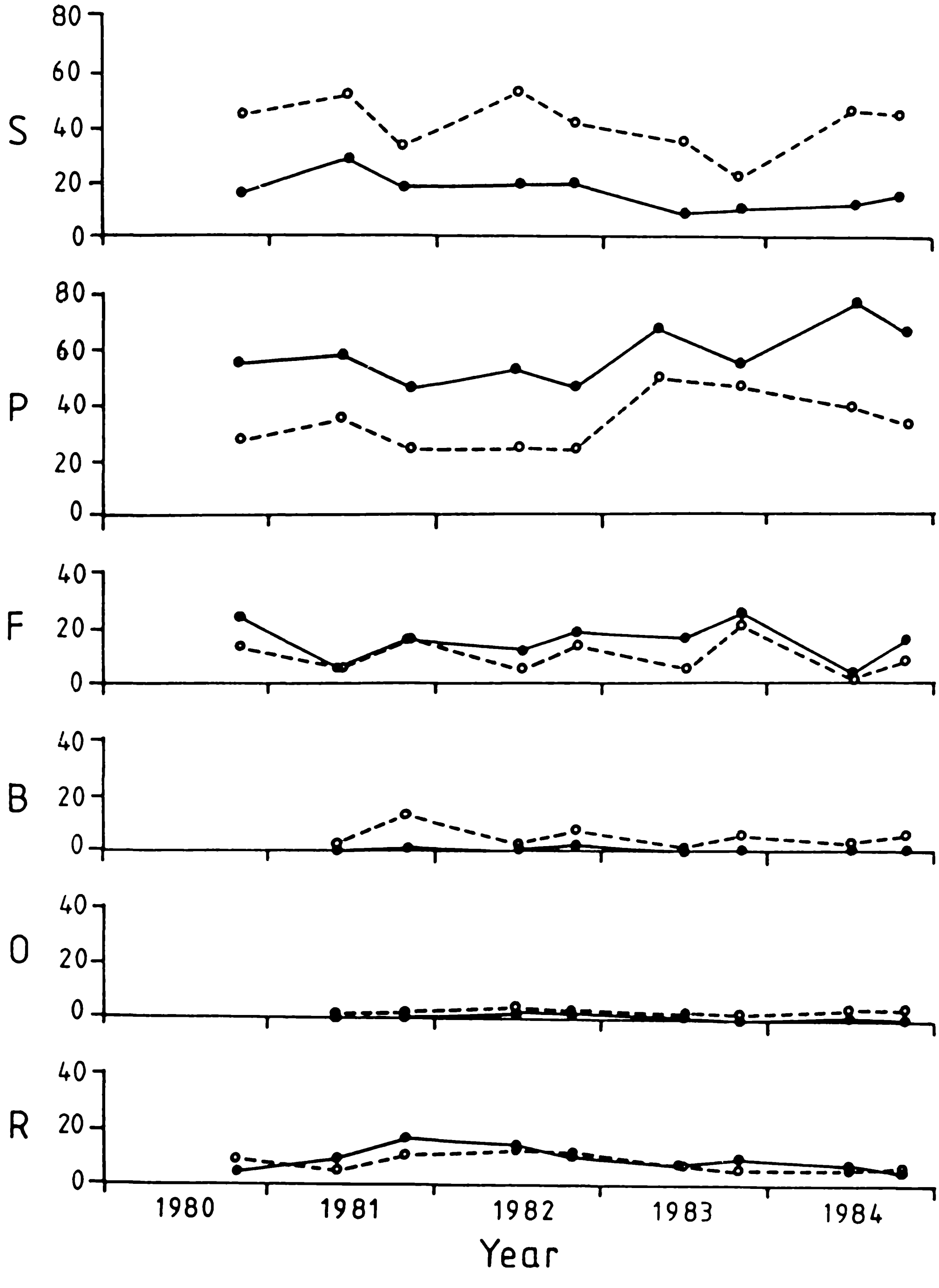


Fig 6:1 Percentage egg survival (S) and mortality caused by parasitism (P), fungae (F), stem boring insects (B), overlaying (O) and remaining factors (R). (o– – –o blackberry, •——• bracken).

presented in Fig 6:2. Block values are used in all statistical analyses except where otherwise indicated.

Figs 6:1 and 6:2 indicate that eggs on bracken have a lower chance of survival than those on blackberry ($t=10{\cdot}00$ $P<{\cdot}001$). From visual comparison of mortality factors in Fig 6:1, it is apparent that parasitism by *Centrodora scolypopae* is the most important mortality factor, usually causing more egg mortality than all other factors combined. No other parasite species was observed. There is a very clear influence of host plant on the level of parasitism with *S. australis* eggs laid in bracken having significantly higher parasitism rates than blackberry ($t=7{\cdot}09$ $P<{\cdot}01$). It is this difference in parasitism levels that is responsible for the variance in egg survival rates between plant species.

There are several different mechanisms that could cause the differing levels of parasitism found in the two plant species. The rougher plant surface could play a role. It is known that plant surface affects the amount of parasitism by *Trichogramma* (Hymenoptera : Trichogrammatidae) (Flanders 1937). Chemosensory perception may be responsible as it is known to be important for many parasites (Fisher 1971). For instance, *Apanteles flavipes* (Hymenoptera : Braconidae) showed preference for the frass produced by stem borers in corn and sorghum rather than from sorghum sudanense, pearl millet and especially sugarcane (Inayatullah 1983). Differing physical structure and hardness of wood in the two species may also be important.

The overall level of parasitism rose significantly in 1983 over the previous years in both bracken ($t=3{\cdot}70$ $P<{\cdot}01$) and blackberry ($t=6{\cdot}54$ $P<{\cdot}01$). In 1984 the study area showed a further increase in parasitism in bracken ($t=7{\cdot}07$ $P<{\cdot}05$; individual plot values) but no change in blackberry, although it was still higher than 1982 and before

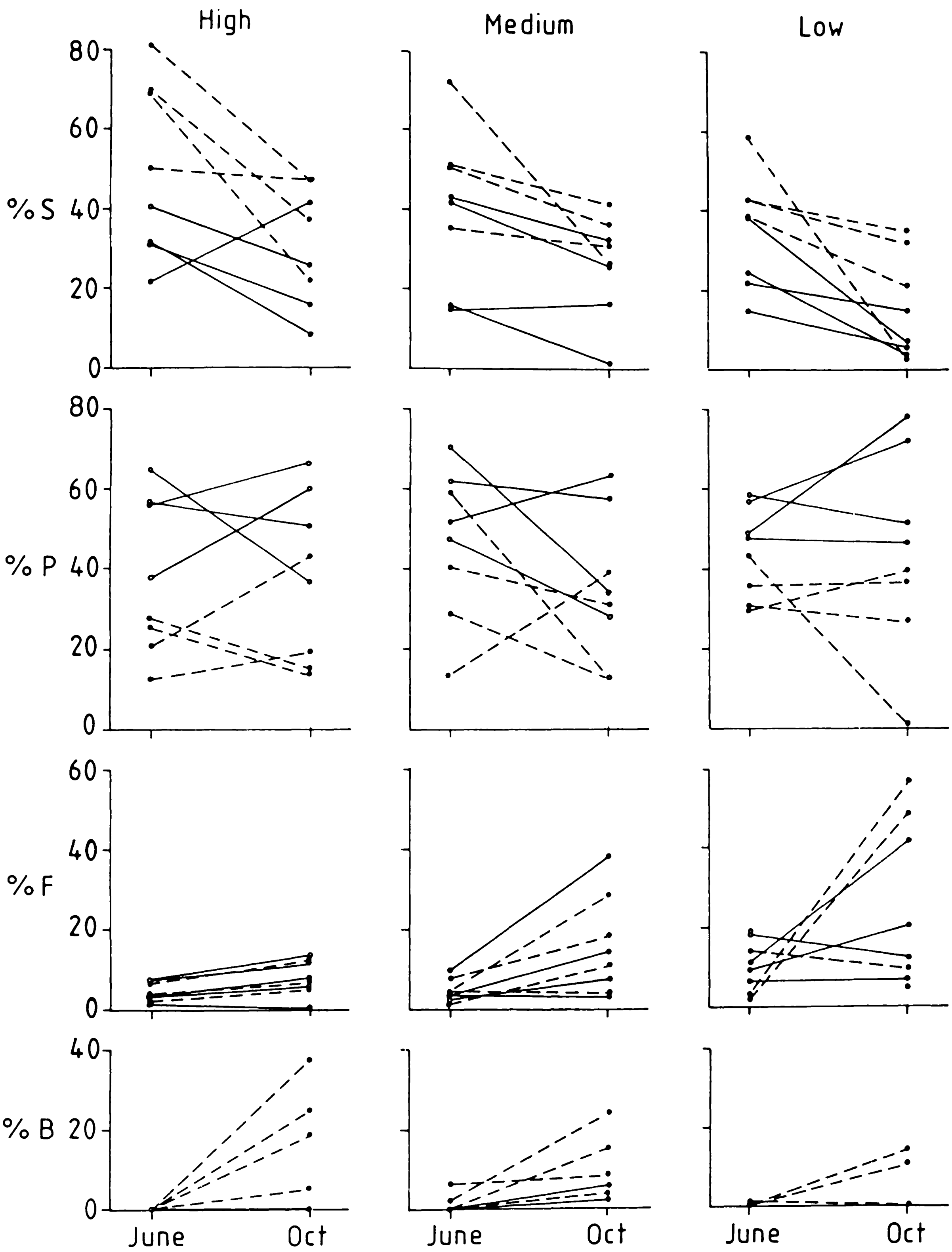


Fig 6:2 Effect of height on egg mortality before and after winter, 1980. (Live eggs (S), parasitism (P), fungae (F), stem boring insects (B), o- - -o blackberry, ●——● bracken. Each line represents one block).

(t=3•21 P<•05). The level of parasitism in all years was higher than those found by Cumber (1966) at sites at Hamilton, Cambridge, Karapiro and Huntly in 1962.

The next most important mortality factor was fungal infection and a complex of fungal species were involved (Table 6:1).

Table 6:1.Fungal species found in egg sample submitted to Plant Diagnostics Division, M.A.F.

Species	Numbers of eggs
Phoma sp.1	17
sp.2	1
sp.3	1
sp.4	1
Aspergillus sp.	10
Pencillium sp.	10
Fusarium sp.	4
Cladosporium cladosporiodes	5
Colletotrichum gloeosporioides	6
Acremonium sp.1	1
sp.2	1
sp.3	1
sp.4	1
Unknown	10

In many cases, the fungi were probably not the initial cause of mortality but were saprophytic fungi that had established after an initial injury. In the course of examining eggs, it was apparent that parasitised eggs were vulnerable to fungal attack from the time of oviposition. Since fungal infection commenced in the vicinity of the oviposition scar, it is likely that the fungal mycelium enters through it. It may be that the parasite female introduces the fungus as spores on her ovipositor. In fungal infested parasitised eggs, the fruiting bodies emerge through the oviposition hole (Plate 6:1). Mature parasite larvae and pupae were also vulnerable.

Saprophytic fungi would also be found in eggs succumbing to factors such as excessive moisture in twigs, overheating in exposed twigs and attack by mite species such as *Pyemotes* which was found by Cumber (1964) to destroy up to 12% of eggs in some localities.

It was difficult to assess whether fungus infested eggs had previously been parasitised and impossible to determine other prior mortality factors. Therefore all eggs containing fungus at the sampling times have been combined in one mortality category in this study.

The incidence of fungal attack had a patchy distribution. Often whole egg batches succumbed to a single species, and eggs on some oviposition sites were more susceptible than on others. Eggs in bracken had a higher incidence of fungal infection than those in blackberry, particularly in 1982 and 1983 ($t=2{\cdot}546$ $P<{\cdot}05$). Possibly this relates to the higher incidence of parasitism on bracken.

Fungal incidence was greatest after winter ($t=5{\cdot}16$ $P<{\cdot}001$). Eggs by then had been exposed to the possibility of attack for up to 9 months during which time the chances of infection were further increased by plant material remaining damp for long periods as a result of reduced sunshine hours and cooler temperatures in the gully.

The third major cause of egg mortality was the destruction of eggs by stem boring larvae. The eggs of *S. australis* are deposited below the outer surface of twigs and stems, often within the central pithy portion. This is the habitat of several species of stem boring Lepidoptera and Coleoptera whose larvae tunnel along stems and destroy any eggs in their path. Such destruction of eggs was greatest after the winter (t=2•47 P<•01) as it is during the late autumn and winter that the tunneling larvae are the largest, occupying the full interior of the stems and causing most damage to the *S. australis* egg population. Eggs in blackberry were most vulnerable (t=3•013 P<•05) with highest levels occurring in 1981 and 1982 when moderate numbers of *Carposina adreptella* (raspberry bud moth) were present. Other stem boring larvae present in both blackberry and bracken were the longhorn beetles (Cerambycidae:Lamiinae), *Navomorpha sulcatum* and *Stenellipses* sp.

Overlaying, or the puncturing of previously laid eggs by a subsequent female, was more common on blackberry than bracken (t=4•558 P<•05), presumably because it is a more preferred oviposition material. With an abundance of oviposition sites available, this was only a small mortality factor rarely exceeding 5% and never approaching the 50% levels mentioned by Cumber (1966).

The remaining egg mortality was caused by an assortment of physical and biological factors, some impossible to identify. A very small number of eggs were infertile. Eggs laid into green plant tissue are susceptible to damage as it twists and shrinks while drying out. Eggs in the current season's blackberry stems were especially vulnerable as stems often split along the oviposition scar either spilling the eggs out or exposing them to predators. Often eggs were found with a shrivelled appearance. This could be caused by desiccation, excessive heat in exposed twigs and predatory mites.

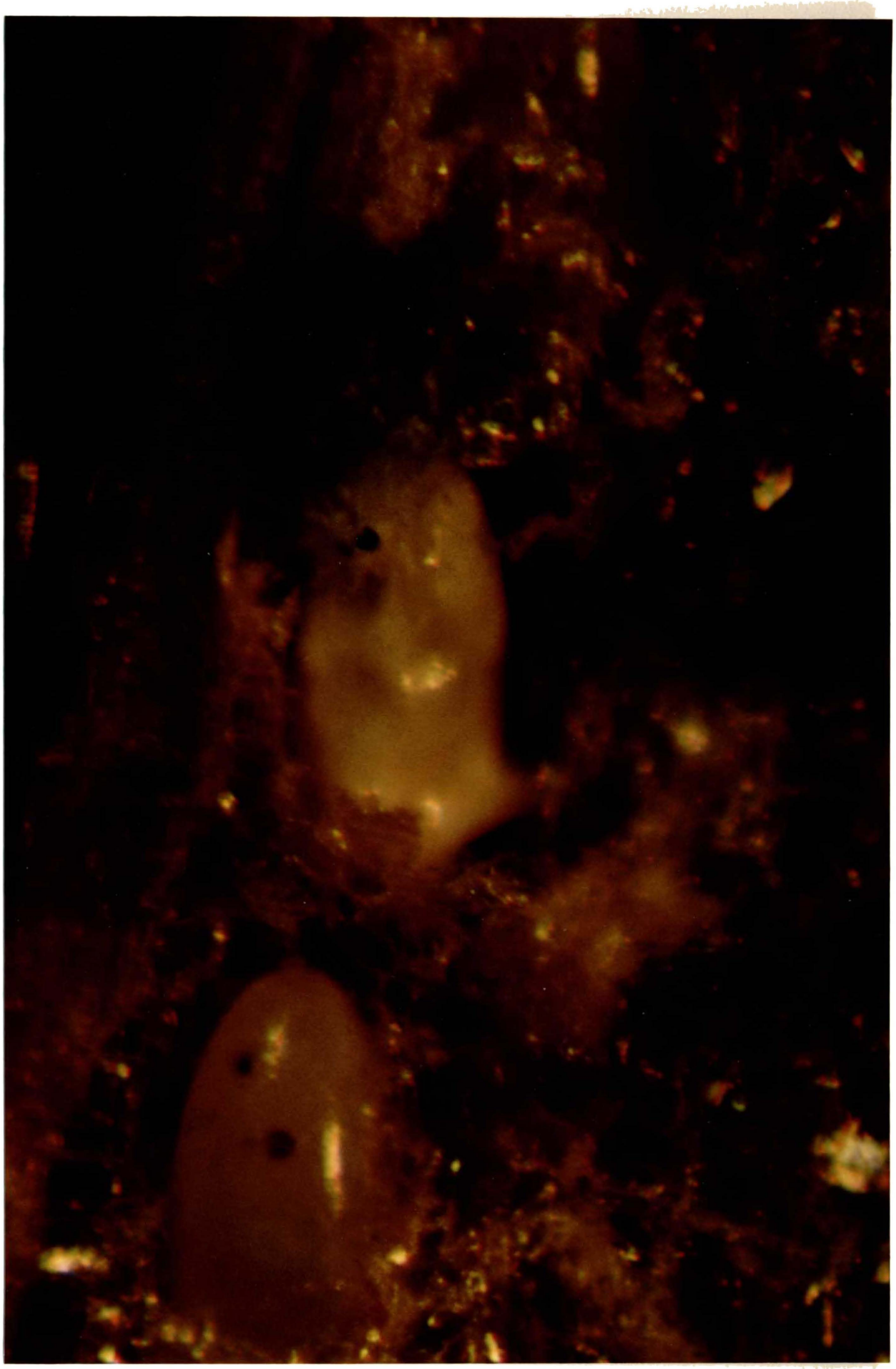


Plate 6:1 Parasitised *S. australis* eggs showing fungal infestation.

mag 120x

When the 1981 results in Fig 6:2 are examined, it can be seen that increasing height above the ground had a positive influence on egg survival with increasing numbers surviving, particularly on blackberry (Analysis of variance P<•01). As found by Williams (1984) in his study on the blackberry leafhopper *Dikrella californica*, levels of parasitism in blackberry were significantly less in the upper canopy than the rest of the vegetation (t=2•362 P<•05) when May samples are compared but it is the response of fungus to height that is mostly responsible for the effect of height on survival. The incidence of fungus increased markedly towards ground level and also after winter (Fig 6:2). In the lower levels of vegetation the plant material is older and possibly already contains high infestations of saprophytic fungi. Humidity would be higher than in the open and woody stems and twigs would take longer to dry out after rain, making a favourable environment for fungi to grow and invade vulnerable eggs.

The only mortality factor to increase with height was the incidence of egg destruction by stem boring larvae, presumably as the plant material most favoured is recently dead plant stems which occur in the middle to upper zones in the vegetation.

CHAPTER SEVEN

NYMPH AND ADULT POPULATIONS

I ANALYSIS OF RESULTS

The assessment of the populations of the nymphal and adult stages of *S. australis* was not as straightforward as for the egg stage. The nymphs and adults are heavily clustered on the growing blackberry and bracken stems between 0.5 to 3 m above ground level. Thus both the number of hoppers per stems and numbers of stems per m^2, were sampled to obtain an assessment of population. Time was the limiting factor in the sampling programme and a compromise had to be made between the degree of precision and the number of samples that could reasonably be obtained by one person. By taking 25 stem samples (bracken and blackberry) per block, an overall population error of about 17% of the mean resulted. The error was lower in years of high population density and near 20% in the 1983-84 season when lowest populations occurred.

In the first two seasons, 3 *S. australis* samplings were taken, one after completion of nymphal emergence, another at mid-summer when most of the population had entered the final instar, and a final sampling of adults at the time of peak oviposition in mid February. The large variation between population values indicated more sampling dates were necessary to evaluate population changes. Consequently in the following seasons 6-9 samplings were taken.

Plant stem samplings were initially taken at only 1 of the *S. australis* sampling dates in each season. However, as with the nymph assessments, the number of sampling times taken in these early seasons was deemed to be inadequate, especially since the stem numbers were found to change over the season. Therefore in 1983-84 and 1984-85, blackberry and bracken stem numbers were assessed at the initial and at least every alternate sampling. The block means of the preceding and following stem assessments were used to obtain a stem assessment for each block at the intervening sampling times. The results and dates of the plant stem assessments are presented in the Table 7:1. For the purposes of this study, the block bracken stem values for the nearest relevant calendar dates in the 1983-84 and 1984-85 seasons were pooled and the resulting stem estimates were used in the calculation of the overall site *S. australis* population assessments that lacked plant data in the first three seasons. In using the pooled data from the 1983-85 seasons in the above estimates, it was assumed that, at each sampling time, the density of the bracken did not vary significantly from year to year. Table 7:1 shows that this was a reasonable assumption. However, from the same Table, it is apparent that the density of blackberry in 1983-84 was significantly higher than at corresponding times in 1984-85. Thus, for the deficient dates in 1981-82, the 1984-85 blackberry data was used, since closer than the 1983-84 data. As the only comparable blackberry assessment in 1981 did not differ from either the last two seasons, pooled 1983-84 and 1984-85 data was used for that season.

Severe time limitations in the 1982-83 season resulted in the exclusion of both blackberry stem and hopper assessments in all but the initial sampling. For population analysis it was desirable to obtain some idea of total nymphal and adult populations using the available bracken data. Thus the proportion of the total population that was on bracken in each block was calculated for each sampling date in the following two seasons. Then by taking the average of the two proportions at dates closest to the time of the corresponding 1982-83

Table 7:1 Bracken and vegetative blackberry stem assessments for study site 1981-85

Season	Date	Bracken	Blackberry
1980-81	19.2.81	5•86±0•40	4•60±0•60
	8.4.81	6•93±0•41	5•17±0•46
1981-82	2.1.82	6•99±0•61	6•51±0•46
1982-83	20.11.82	5•40±0•35	7•84±0•99
1983-84	13.11.83	4•79±0•45	14•76±1•70
	15.12.83	7•48±0•71	13•76±1•50
	17.1.84	7•58±0•62	11•60±1•12
	14.2.84	7•60±0•62	4•42±0•52
1984-85	20.11.84	4•31±0•72	7•45±0•62
	2.12.84	6•40±1•10	6•70±0•56
	1.1.85	6•80±0•98	5•08±0•33
	30.1.85	7•53±1•65	5•52±0•58

bracken population assessment, a very rough estimate of the total population was calculated. These estimates assumed that the distribution of hoppers between plant species did not alter at the equivalent dates from season to season. This assumption was not unrealistic as shown by comparing percentage of the population on bracken and blackberry at the early January sampling in each of the other 4 seasons (Appendices 13, 14,16 and 17). In three of the four years, the percentage on bracken was 65-67%, with only 1983-84, with high blackberry stem numbers, showing a noticable difference at 55%.

In all assessments of hopper and stem numbers, the distributions did not markedly depart from normality, so to simplify subsequent data analysis, arithmetic means only were used and there was no transformation of data. The standard errors were assessed from plot differences within each block. Overall means are weighted, taking into account the differing block sizes.

In each hopper sample, the number of each instar was counted. For ease of analysis and presentation, the average level of development or 'mean instar' (m.i.) for each plot and block was calculated where:

$$\text{m.i.} = \frac{\Sigma \text{ No. individuals/instar x instar no.}}{\text{total individuals}}$$

and where instar no. varies 1 for first instar to 6 for adults. This method has been used successfully with black beetle *Heteronychus arator* (Coleoptera:Scarabaeidae)(R. Watson pers. comm.) and by the author with *Inopus rubiceps* (Diptera:Stratiomyidae) (Gerard and Burton 1983).

The standard errors were assessed from plot differences rather than stem differences. The variation between blocks in m.i. values was tested using analysis of variance (ANOVA) and where a significant F value was found, the statistical significance of the differences between means was tested by comparison with the Least Significant Difference (LSD)(Snedecor and Cochran 1967). In the first two seasons with only 2 usable sampling dates, individual plot values were used but in the subsequent seasons, block values sufficed.

II NYMPHAL AND ADULT ASSESSMENTS

The block mean numbers of *S. australis* individuals per stem and calculated density per m^2 at each sampling for every generation are listed in Appendices 13-17. Fig.7:1 shows the mean number of *S. australis* individuals per bracken stem found in the study area between 1980-85. This is a measure of population intensity only, as the proportion of the total population on bracken changes throughout the season and stem numbers alter within and between seasons. Nevertheless, the figure shows that the population intensity was very much lower in the 1983-84 season than in previous years. A small recovery is apparent in 1984-85.

The increasing importance of bracken as a host plant as the season progresses can be seen in Figs 7:2-3. These show the overall assessments of hoppers per m^2 as well as the bracken and blackberry contributions to the populations in each block over the last two generations. The data from the earlier generations also followed the same pattern (Appendices 13-15). In November and early December the majority of the young nymphs are found on the abundant, succulent, vegetative blackberry stems. When vegetative growth diminishes as flowering buds are produced, the nymphs and particularly the adults,

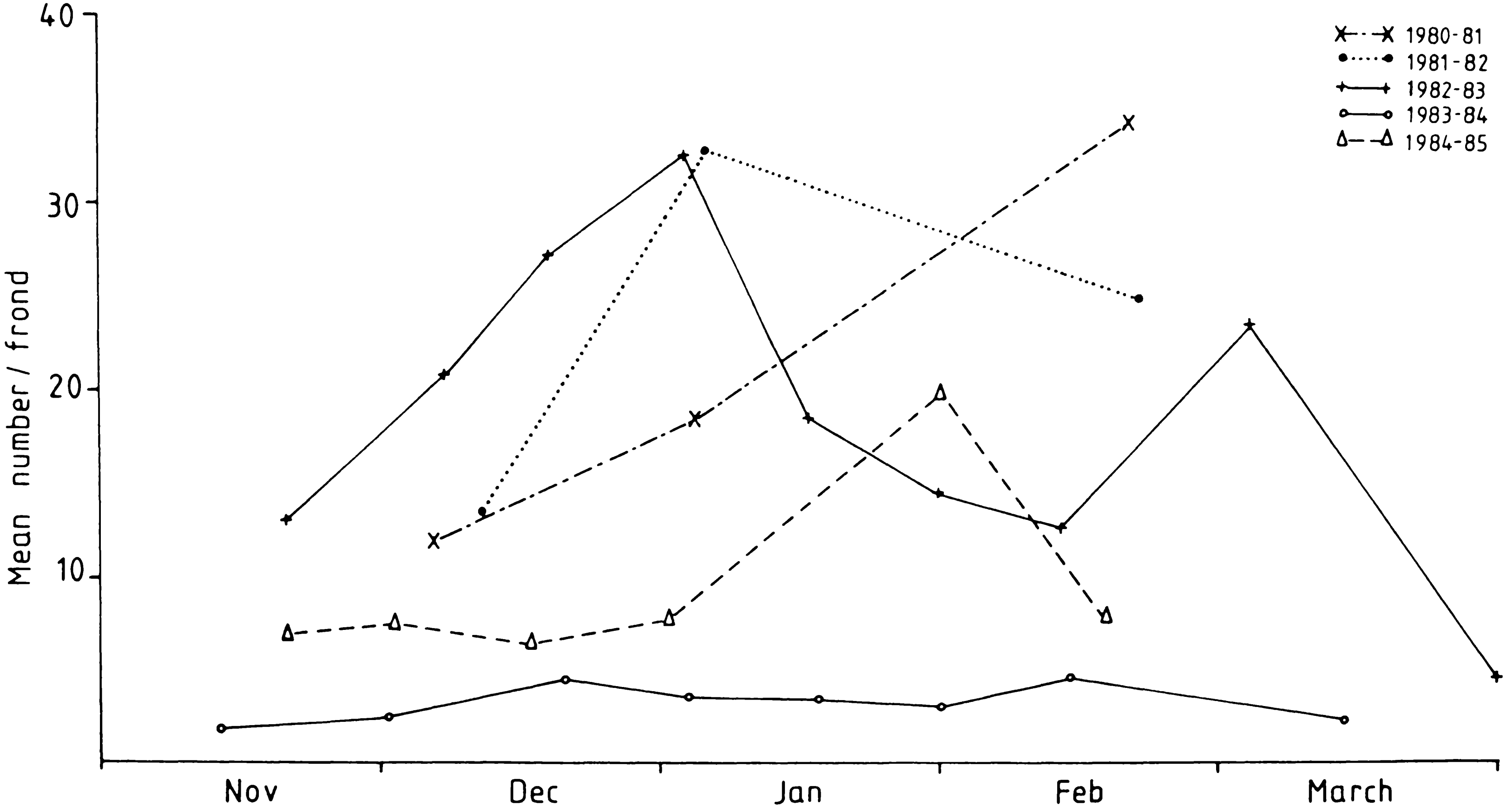


Fig 7:1 Mean number *S. australis* per bracken frond at Steele's Farm 1980-1985.

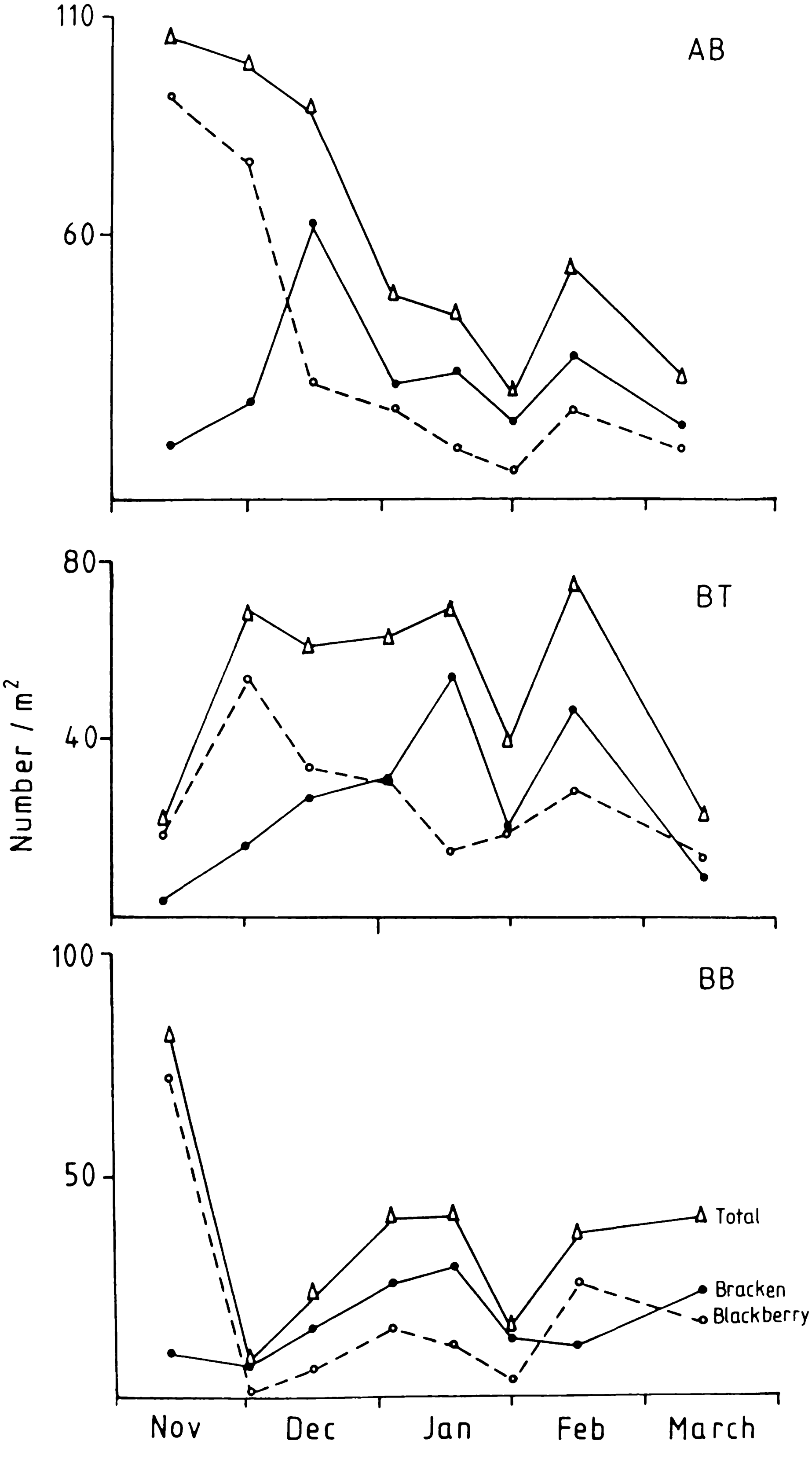


Fig 7:2 Mean numbers of *S. australis*/m^2 in each block 1983-84.

(Block AT destroyed during previous winter).

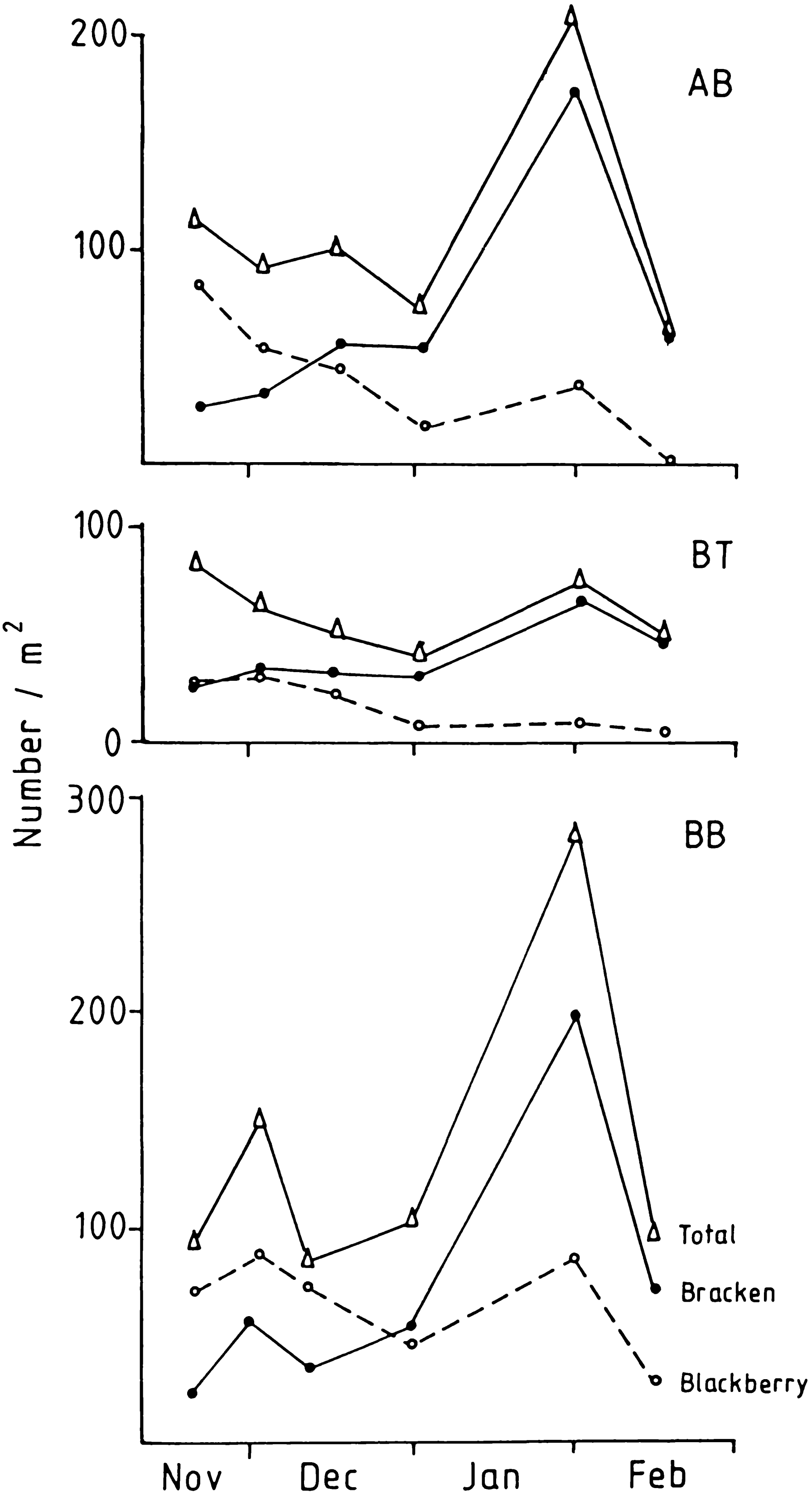


Fig 7:3 Mean numbers of *S. australis*/m^2 in each block 1984-85

move onto the bracken. High numbers of adults are found on the few prematurely dying bracken stems during late summer.

The population levels show considerable fluctuations within and between blocks in a single season (Figs 7:2-3). The blocks are not isolated from each other or the gully as a whole, so dispersal, especially by adults, occurs readily. It is likely that dispersal between blocks contributes to the observed fluctuations although they may be artifacts of the large errors associated with these assessments. Therefore it was not considered possible to draw any firm conclusions on block population differences and the data were pooled to investigate population trends in the study area as a whole.

Fig 7:4 shows the overall mean numbers of *S. australis*/m^2 in the study area over all seasons, including the 'theoretical' estimates for 1982-83 when only bracken was sampled. If that year is excluded, the fluctuations apparent in the blocks have mostly disappeared with the pooling of the data. The conclusions that can be drawn from the figure are similar to those from the bracken stem data alone (Fig 7:1). The 1983-84 nymphal and adult populations were substantially lower than the preceding years and the 1984-85 nymphal population does not show full recovery to former levels. However, a peak at the end of January 1985 suggested inward migration of adults, which could hasten the increase in numbers.

It is apparent, from Fig 7:4, that the nymphal and adult stages do not appear to suffer any gross mortality over the summer. Inward migration could keep numbers up, although there is no apparent reason why adults would move onto the study area in preference to other areas in the gully. Very few mortality agents were seen in operation, in contrast to populations of grassland Auchenorrhyncha leafhoppers (Waloff 1980), in which large numbers of predators and parasites are

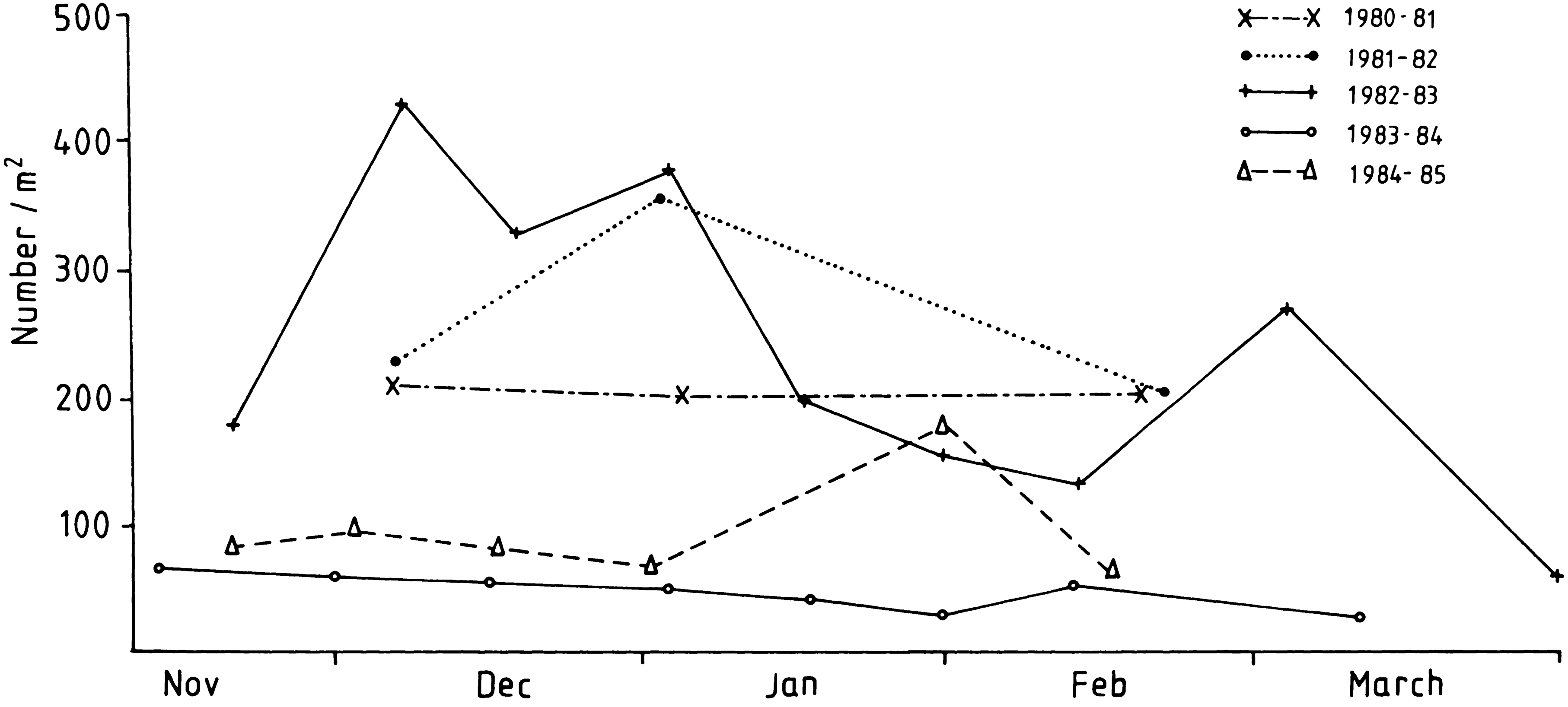


Fig 7:4 Mean number S. australis / m^2 at Steele's Farm 1980-1985

(Std errors in appendices)

found. Adults were trapped by spider webs but the numbers were very low compared to the total population. Three Hemipteran predators were observed feeding on *S. australis* nymphs; a nabid *Nabis* sp. and two pentatomids, *Oechalia schellembergii* and *Cermatulus nasalis*, both of which also occur in Australia. No parasites of nymphs or adults were found although only adults were dissected in any number. Bird predation probably occurred but was not observed in spite of attempts to do so. A very small number of nymphs and adults were found dead with visible fungal infestation. It was thought that fungae such as found by Siew (1960) (*Trichothecium roseum*, *Hymenostilbe* spp. and *Hirsutella citriformis*) may be responsible. However, *Glomerella cingulata* was isolated from the specimens sent to Plant Protection Centre, M.A.F. Auckland. This is a common saprophyte or weak parasite of many plants and was considered to have infected *S. australis* after death. These individuals probably were victims of the hemipteran predators which leave no easily visible damage. The low incidence of fungus may have been due to the low humidity in the gully during summer.

III RATE OF DEVELOPMENT OF S. AUSTRALIS IN THE FIELD

The block m.i. values of *S. australis* on bracken and blackberry are listed in Appendices 18 and 19. The blocks AT and AB had significantly higher m.i. values than the B side blocks well into January in all years (ANOVA $P<\cdot01$). Block AT values exceeded those of Block AB in 1980-81 (LSD 1%= $\cdot33$ $P<\cdot01$) and in 1982-83 (LSD 1%= $\cdot23$ $P<\cdot01$) after which AT was unfortunately eliminated from the study. The two site B blocks showed no significant within season differences in any year.

The m.i. values in 1980-81 and in 1984-85 were at higher levels than in corresponding times in all other years. These differences are more apparent in Table 7:2, showing the m.i. values for all blocks (blackberry and bracken) at the nymphal sampling taken 2-4 January each year. When analysis of variance was carried out on the 1981, 1982 and 1983 plot results and the differences between the means tested by LSD , each year differed significantly from the others (P<·05) with 1983 being the lowest and 1981 the highest. When the same tests were repeated for all years, but omitting AT results, it was found that 1985 exceeded all years (P<·01) and 1983 was less than all (P<·05). 1984 did not differ from 1982 and was less than 1981 (P<·05).

Table 7:2 Mean instar (m.i.) of *S. australis* population in each block 2-4 January 1981-85 (* sample taken 9.1.82, ns not sampled).

Date	Bracken				Blackberry			
	AT	AB	BT	BB	AT	AB	BT	BB
1981	4·90	4·56	4·16	4·19	4·73	4·42	4·06	3·97
1982	4·57	4·57*	3·78	3·52	4·27	4·28*	3·67	3·42
1983	4·20	3·93	3·67	3·63	ns	ns	ns	ns
1984	ns	4·47	3·87	3·71	ns	4·12	3·80	3·91
1985	ns	5·12	4·86	4·79	ns	4·91	4·79	4·81

(standard errors given in Appendices)

The difference in m.i. between plant species, apparent in Table 7:2, occurred in all samplings taken earlier in the season. When same day bracken and blackberry m.i. values from the same block are paired (differing day values excluded), a highly significant difference was found (t = 6•855 P<•001), with the blackberry m.i. value averaging 0.175±.026 below that of bracken.

1, Interpretation of m.i. results

The differences between gully sites in m.i. values of the nymphs sampled on the same day is easily explained by the aspects of each site. Site A, facing N.W., receives more direct sunshine and recorded higher temperatures than site B facing the S.E.. This can be seen in Fig 7:5 showing the monthly cumulative day degrees calculated from temperatures recorded in blocks AT and BT. In every month recorded, the monthly day degree total in block AT exceeds that of BT. The site A nymphs hatched before those on side B. For instance, on 6.11.82, 100% of eggs from 20 egg batches collected from AT had hatched, compared with 71•6±8•9 in BT. Even two weeks later, on the 20.11.82, only 95•6±2•3 eggs had hatched in BT. The difference in maturity, initiated by the earlier hatching of site A nymphs, is maintained throughout the season by the higher temperatures on site A until the majority of the population are adults.

The differences between years is also temperature related but not so clearly discernable because the temperature records in the gully were not initiated till March 1982. Data was obtained from the nearby Rukuhia Airport, but as can be seen in Fig 7:5, the cumulative day degrees recorded in the gully were much higher, partly because it was sheltered from wind. Nevertheless, the Rukuhia data does indicate yearly fluctuations. The coldest summer was 1982-83 with a total of 624 day degrees recorded from the time of first nymphal appearance till

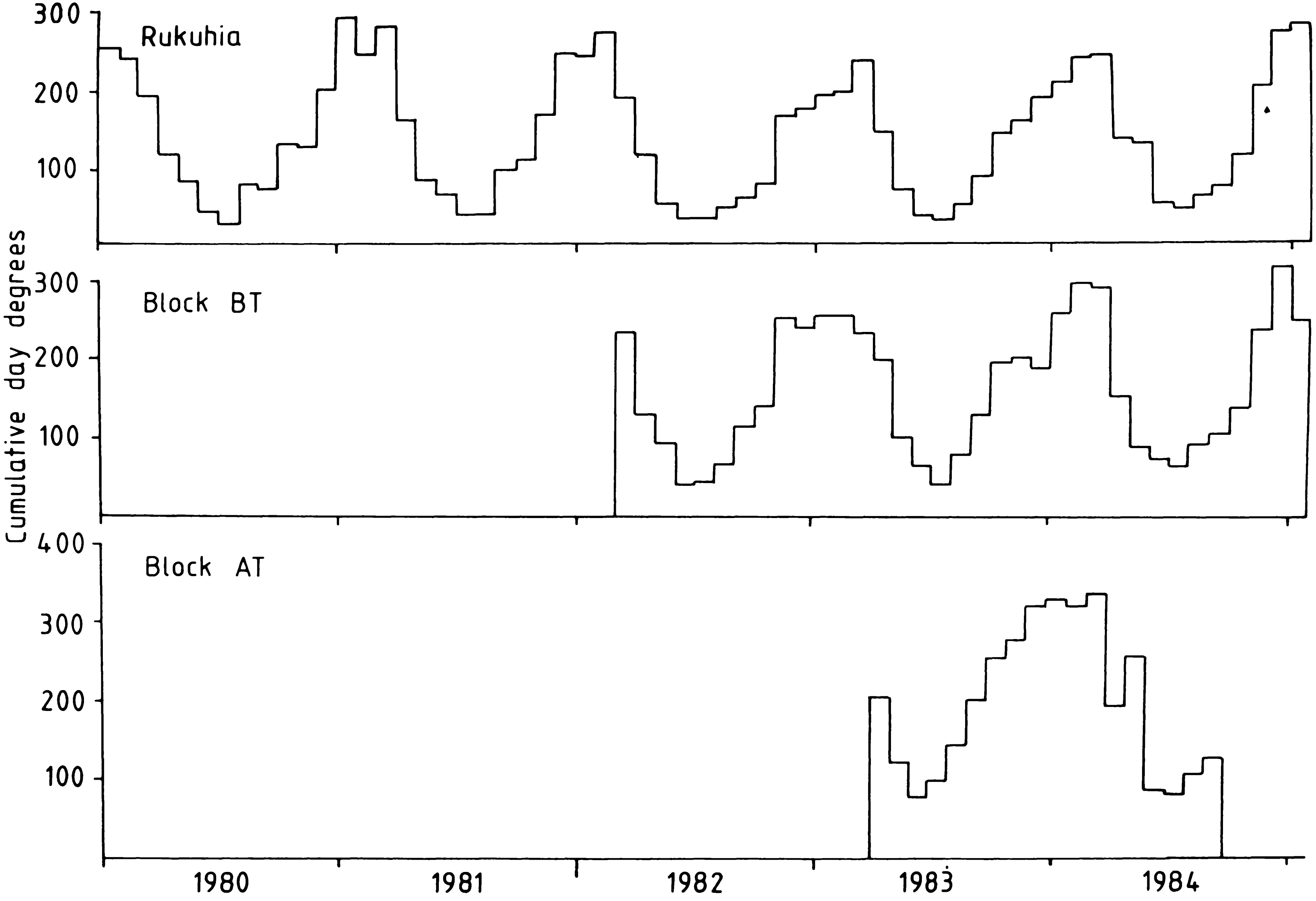


Fig 7:5 Cumulative day degrees at Rukuhia and study area, 1980-84. (10°C lower threshold).

mid February (usual time of peak oviposition). This compared with 838 in 1981-82, 754 in 1983-84, 845 in 1980-81 and over 900 in 1984-85. These figures match the order found in the analysis of block m.i. results which were presented in Table 7:2.

The m.i. values from 1982 onwards in block BT can be compared directly with the cumulative day degrees calculated from the temperature data recorded in that block. Fig 7:6 shows that, in every month, the nymphal development in 1982-83 was substantially behind the development of the 1983-84 population, which in turn was behind 1984-85. Of particular importance is that the 1982-83 population did not reach full maturity until March, compared with mid February for 1984 and the end of January in 1985. The 1984 rate of development was found before not to differ from 1981-82 and to be behind that of 1980-81. Thus the maturity date of the 1982-83 is also likely to be behind that of all other years as well. Delay in population maturity would result in a shorter time available for oviposition, before cold temperature inhibition, compared to other generations.

Fig 7:7 shows that the differences in population development between years disappears when m.i. values are compared with day degrees experienced, at least over the early nymphal stages. The later divergence could be caused by factors such as varying plant vigour and rainfall.

From the plant species variation in Table 7:2, it appears that nymphs develop at a slower rate on blackberry than on bracken. Initially most of the population is on blackberry (Figs 7:2-3)(Appendices 13-17), but moves onto bracken as flowering buds are produced on blackberry. It is possible that this species difference could be accented by the older individuals migrating first, but as the difference appears from the earliest samplings, it is reasonable to

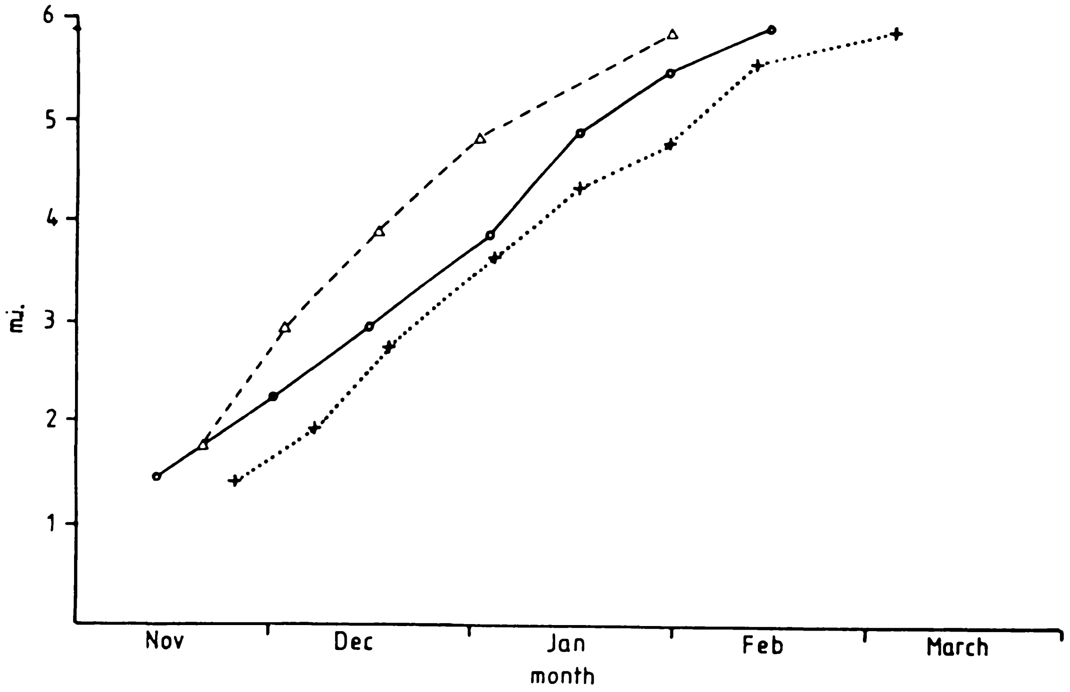


Fig 7:6 Relationship between Block BT m.i. values and date of sampling.

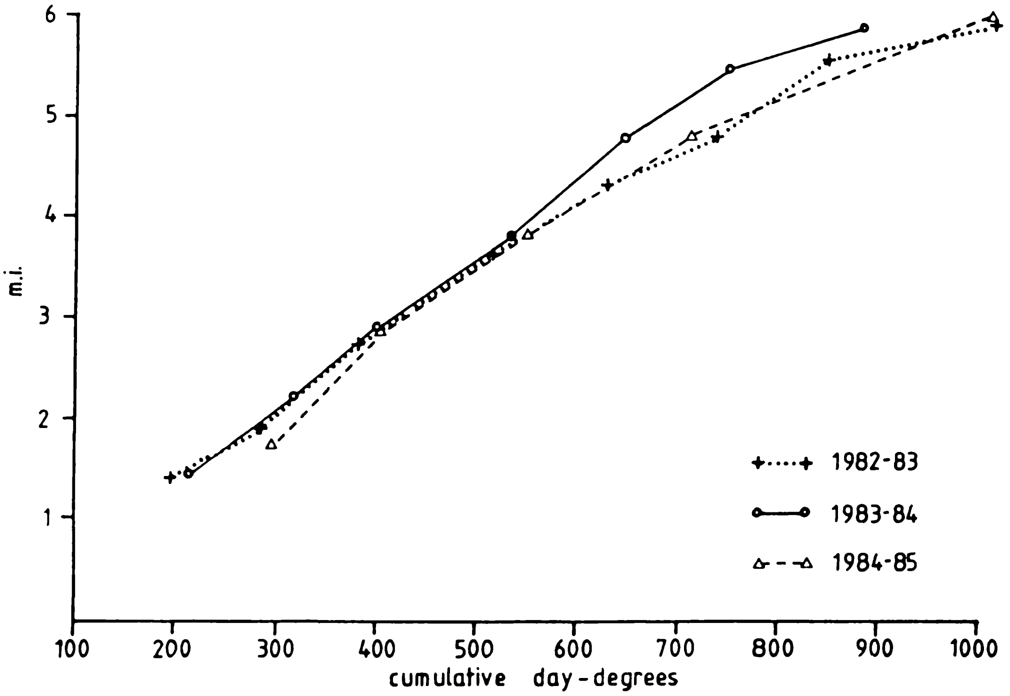


Fig 7:7 Relationship between Block BT m.i. values and cumulative day degrees.

assume that bracken is a better nutrient source than blackberry.

IV DISCUSSION

The population levels of nymphs and adults fell in 1983-84 following a large reduction in egg population numbers (Chapter 5). The slow nymphal development in 1982-83, compared to all other years, provides an explanation. In 1983, the population did not reach full maturity (100% adults) till March, compared to mid February in 1984 and the end of January in 1985 (Fig 7:6). This would have resulted in a shorter oviposition period than in other years. *S. australis* females produce eggs in up to three sequential egg batches with several weeks between each (Siew 1960). The delay in commencement of oviposition would result in many females producing below their optimum capacity and resulting in low egg numbers at the start of the next generation. It is also possible that cold summer temperatures could reduce the size of egg batches produced by females, either directly or by affecting host plant nutrient value, but this is pure speculation. The very close relationship between development and cumulative day degrees experienced (Fig 7:7) indicates that temperature data could be used to predict the commencement of oviposition and the possible rise or fall of the next *S. australis* generation.

The switching of host plants through the season has been noted before in leafhoppers. Species of grassland Auchenorrhyncha leafhoppers have been found to prefer a narrow range of soluble N levels. As the plant N-levels altered (associated with flowering, seed setting and senescence), leaf hoppers switched onto other food plants that had suitable N levels (Prestidge and McNeill 1983). The observed shift by *S. australis* from blackberry to bracken could be a similar response to changing nutrient levels. However, analysis of samples of bracken and blackberry stems for N content did not give evidence of this. Five stems of either vegetative blackberry, flowering blackberry, young bracken at the crozier stage and older bracken with most pinnae fully expanded, were weighed and chopped coarsely. Five gm. of each was then extracted by maceration in 30 ml. of 5% trichloroacetic acid and analysed for nitrogen content at the Nutrition Centre Laboratory, Ruakura Agricultural Research Centre, using Kjelfoss equipment. The remainder was oven dried to obtain % dry matter per sample. The results are presented in Table 7:3.

Table 7:3 Nitrogen levels in blackberry and bracken during *S. australis* nymphal stages:

	% N dry weight.
Vegetative blackberry	2•09±0•31
Flowering blackberry	1•75±0•09
Crozier stage bracken	3•37±0•24
Bracken with expanded pinnae	1•86±0•11

The bracken N levels, when multiplied by the standard conversion of 6.25, did not differ form those in Lawton's (1976) summary of available data on changes in crude protein levels in bracken through the growing season. He found that, although protein content fell through the season, both total insect numbers and species diversity increased. Young bracken contains high levels of toxic thiamase and cyanide which diminishes as the season progresses and he thought the effects of these are sufficiently great to over-ride the changes in "food quality".

Flowering and vegetative blackberry and the older bracken have similar levels of N content (Table 7:3) and high numbers of young nymphs are found on bracken in the crozier stage. It is possible that physical differences alone give rise to the preference for bracken as the season progresses. Blackberry stems become lignified as flower buds are produced and contain little sap, so *S. australis* hoppers are likely to move to more hospitable stems. Since vegetative blackberry becomes less common as the season progresses, most of the population is then found on bracken.

The preference of adults for senescing plant tissues is thought to be a response to the resulting rise in soluble compounds and a higher ratio of amino acids to sugars (Siew 1960), conditions favourable for oviposition. The previously mentioned grassland species showed a response in oviposition rates as N increased (Prestidge 1982). Metcalf (1970) correlated increased fecundity of *Saccharosydne saccharivora* Westw. (Homoptera:Delphacidae) to an increase in plant N levels and similar results were found with other leafhoppers by Hinckly (1963) and Fennah (1969).

The variation in m.i. values between species is likely to be caused by bracken being a better nutrient source than blackberry. Prestidge (1982) found an optimum range of soluble N existed above or below which instar duration of Auchenorrhyncha leafhoppers was lengthened. Perhaps bracken is closer to the optimum for *S. australis* than blackberry in its early growth stages. However, it must be remembered that nymphal rate of development depends on a wide range of factors, of which N content of a plant may be only one small part.

CHAPTER EIGHT

FECUNDITY OF SCOLYPOPA AUSTRALIS

S. australis females are synovigenic, that is the newly moulted females do not contain mature eggs initially, but produce them during their adult life. Siew (1960) studied the reproductive biology of *S. australis*. He found that the late instars had well developed ovarioles, containing 3-4 oocytes but it was not until the 13th day after moulting that a distinct chorion was visible on the terminal eggs. Copulation occurred two weeks after moulting and the first oviposition 2-3 days later. Dissections of mature females showed a potential fecundity of between 16-48 eggs with the maximum frequency of 32. Females generally did not lay their full complement of mature eggs in a single egg batch and so batch size could not be used as a indication of fecundity. No cessation of ovarian development was observed and Siew (1960) considered that 3 times the initial egg complement could be produced in a female's lifetime although some reduction in numbers was possible as the female aged.

The continual production of eggs by the female over several months made assessment of fecundity difficult. Dissection of females collected at intervals from the study site over the 1981 oviposition period showed that average egg content ranged between 10-18 eggs with no notable decrease until mid April when many adults had already died. (Appendix 20). The maximum number of potential eggs found in a single female was 50. The results in Appendix 20 clearly do not give an indication of lifetime fecundity of *S. australis* females.

It was apparent that in order to obtain a fecundity estimate, females would have to be caged for the duration of their oviposition period. In order to maintain adults alive for that length of time, it was found necessary to have cages large enough to accommodate a growing plant shoot or portion thereof, the cages needed to be placed in a sheltered position and above all, to be bird proof. A cage trial in 1983 had to be abandoned after birds had torn holes in plastic portions of every cage, the design of which had seemed to be very practical in tests in the home garden.

Early in the 1984 oviposition period, sleeve cages were made of curtain netting, 25 cm long and 15 cm wide, and were slipped around young raspberry canes growing in the author's garden in Hamilton. Mating pairs of *S. australis* adults were collected during the evening of 17.2.84 and one pair was placed in each of the cages which were then tied securely at each end around the stems. The adults were then left till the end of the oviposition period (24.5.84) when the number of eggs per female was counted.

A similar procedure was repeated in the study site. However, the site was precarious even during the day and an attempt at collecting mating pairs there was considered foolhardy. Garden females were not used as it was thought nutrition prior to mating may influence fecundity. Instead, females that by eye appeared young were trapped and placed in sleeve cages, with two males, on either bracken and blackberry. The following week, any cages with dead females were removed and excluded from trial results. The remaining cages were left till the end of the oviposition period.

The number of eggs laid by each female is given in Table 8:1. The average egg number laid by the suburban females on raspberry was high (221±61 n=13), far exceeding those from the study site (bracken 48±13 n=11, blackberry 38±14 n=7). Part of this difference may have been caused by the host plant influencing the nutritional intake of the

Table 8:1 Number of eggs laid by females caged on raspberry, bracken or blackberry plants during the 1984 oviposition period.

Plant		
Raspberry	Bracken	Blackberry
111	44	40
188	11	76
210	12	23
235	80	20
205	12	31
19	136	0
277	29	53
206	17	
197	41	
356	117	
323		
243		
301		

females. The relative shelter in the garden may have provided a better environment than experienced by field adults. Above all, the field females may have oviposited prior to capture. In spite of the low numbers involved, the suburban females do give an indication of the potential fecundity of *S. australis*. It was notable that survival was high in the garden females with the first death recorded 53 days after mating and 8 females were still alive when the experiment concluded, 95 days after mating. No field adults survived till collection time. Significant correlations between fecundity and longevity have been found in *Errastunus ocellaris* (Fallen)(Homoptera:Cicadellidae) and *Stenocranus minutus* (Fabricus)(Homoptera:Delphcidae)(Waloff 1980). The long length of life of the garden females would have contributed to the number of eggs laid.

Delong (1971) in a review of leafhopper bionomics, found that fecundity was generally 100-200 per female but ranged from 16 to over 1000. British grassland Auchenorrhycha have been studied intensively and the fecundity of Cicadellidae species was found to range from 25-189 and the Delphacidae from 88-360 (Waloff 1980). Although only a small number were studied, the fecundity of *S. australis* appears to be typical of most Auchenorrhychan species.

CHAPTER NINE

POPULATION DYNAMICS OF SCOLYPOPA AUSTRALIS

I INTRODUCTION

In the past, population ecology was dominated by debate amongst those working in that field. Some, such as Nicholson (1954), considered that populations were governed by density dependent mechanisms and biotic elements in the environment. Other authors, such as Thompson (1956) and Andrewartha and Birch (1954), held that the primary mechanisms controlling population size were density independent factors, eg weather. Nowadays it is widely accepted that the theories are not necessarily contradictory. A full range of types of population dynamics can be recognised from the r-strategists, existing in unpredictable environments, having high capacity for population increase (high r values) and being poor competitors, to the K-strategists, living in fairly stable environments, having relatively low levels of increase and being good competitors (MacArthur and Wilson 1967). Southwood and Comins (1976) and Southwood (1977) developed a synoptic model based on natality, intraspecific competition and natural enemy action which varies along this r-K continuum. Between the two extremes of r- and K-strategists is the natural enemy ravine where predator and parasite effects are most significant. The model indicates the most effective agents are those with the widest ravine, which has had practical relevance to biological control programmes.

Extensive reviews of factors regulating populations have been made by Solomon (1949, 1964), Clark et al. (1967), Richards and Southwood (1968), Varley et al. (1973) and Price (1975). Density independent mortalities include both catastrophic factors which produce very variable mortalities, as well as those that vary very little (Varley and Gradwell 1970). Often these can be caused by weather (Solomon 1960) although food availability, parasites, predators and disease can have a density independent effect. Mathematical population models with only density independent mortalities are unstable (Varley and Gradwell 1970).

Density dependent mortalities can regulate populations at a stable equilibrium density, in stable cyclic oscillations or even apparently chaotic population fluctuations (Hassell et al. 1976). Such mortalities include certain predators, parasites and pathogens and inter- and intraspecific competition for resources (Clark et al. 1967).

Over the past two or three decades, ecologists have become more interested in studying the dynamics of individual populations or populations of several interacting species. For many, the emphasis has been on the theoretical modelling of variables that determine population levels so that the effect of changes in such can be predicted through computer simulation (Holling 1963, Varley and Gradwell 1970). Here the aim is to understand the basic underlying principles of population dynamics. On the other hand, complex models using life table data have been produced for pest management control. Many have been for aphid populations, e.g. Hughes (1963), Hughes and Gilbert (1968), and Gutierrez (1984). Because of their complexity, these models are not easily amenable to the mathematical manipulations involved in the theoretical investigations of ecological principles.

Mathematical models enable rapid answers to questions that would have otherwise required long term ecological studies and are powerful tools in the management of pest populations. However, not all issues of concern to ecologists can be solved entirely by computer simulation and theoretical models can be limited by the lack of understanding of the many biological processes and interactions involved in insect population dynamics. Eventually it will be from detailed studies of natural populations and the accompaning field and laboratory experiments designed to elucidate the biological processes involved, that solutions will come for many of the issues under debate in population ecology.

Life table and key factor methods of population analysis have been developed by Morris (1955, 1957) and Varley and Gradwell (1960) and are reviewed by Southwood (1966, 1978). These are quantitative, multifactor approaches and depend on sound population estimates. A life table tabulates the population density at different stages of the life cycle from egg to adult, as well as fecundity if possible. From a series of life tables, it is possible to identify quantitatively the age specific mortality factors that are important in determining the population size. The difference in the log density of the population before and after a mortality factor acts is called the k value of the mortality. Total generation mortality K, is given by

$$K = k_0+k_1+k_2+\ldots\ldots ki$$

When plotted over a number of generations, often one or more of the k factors can be seen to be key mortality factors that are responsible for the flucutations in a population from generation to generation (Morris 1959, Varley and Gradwell 1960, 1970).

The use of graphical key factor analysis is restricted to populations with more or less discrete generations. Where populations overlap, a number of techniques, often complex, have been developed (Birley 1977, Bellows and Birley 1981, Hughes 1963, Manly 1974).

The basic aims of the following section are to use the estimates of the population of *S. australis* presented in the previous chapters to construct life tables and analyse them to discover what are the most important factors determining the fluctuations in the population.

II CONSTRUCTION AND ANALYSIS OF LIFE TABLE

Life tables were constructed for five generations of the *S. australis* population in the study area from 1980-1985. The population values used were the pooled data from all blocks although block AT had to be excluded from mid 1983 onwards. *S. australis* is univoltine, overwintering in the egg stage which lasts about 9 months. The first appearance of each stage occurs about the same time each year but within the population, the nymphal instars overlap to some degree. It is often possible to calculate an estimate of the number of individuals entering a specific stage (Southwood 1978) and methods used for Auchenorrhyncha leafhoppers are given by Richards and Waloff (1954,1961) and Waloff (1980). However, as there were already large errors associated with the nymphal and adult estimates and as results indicated that mortality during these stages was low, it was considered that time specific rather than age specific intervals would serve the purposes of this study. The time intervals used and the k values then calculated are shown in the life table for the 1982-83 generation (Table 9:1). The egg stage was sampled in October 1980, June 1981 and in both these months in subsequent years. Both times are presented in the life tables. The early time gives the number of total eggs laid and numbers surviving parasitism. The later sampling gives the number of eggs surviving till egg eclosion. The total number of eggs found in the October 1980 sampling was used as the figure for eggs laid in June 1980, and the number of eggs not parasitised (although perhaps now dead

Table 9:1 Life Table for 1982-83 *S. australis* generation.

Time	stage	No./m^2	log. N	k
	Potential eggs	22321	4·349	
			k_0 (variation in natality)	0·019
June 82	Eggs laid	21400	4·330	
			k_1 (parasitism)	0·428
June 82	Eggs surviving parasitism	7984	3·902	
			k_2 (winter mortality)	0·301
Oct 82	Eggs surviving winter	3987	3·601	
			k_3 (neonate nymph loss)	0·898
Nov 82	Early instars	435	2·638	
			k_4 (nymphal mortality)	0·057
Jan 83	5th instars and first adults	381	2·581	
			k_5 (adult loss)	0·460
Feb 83	Adults at peak oviposition	132	2·121	
				K = 2·197

from other causes) for the number of eggs surviving parasitism. Both of these are likely to be underestimates as egg batch number usually decreases over winter.

Sometimes, because hatching was not yet completed, the number of nymphs/m^2 in November was exceeded by the early December assessment. In such a case, the latter estimate was used.

The life table was analysed by the methods of Varley and Gradwell (1960) and Smith (1973). Fecundity data was not obtained from the site in most years. Incomplete budgets from eggs to adults can still be used to determine the relative importance of mortality factors in determining the size of the adult population (Southwood 1966). The above k factors were plotted against generation so that key factors can be identified by visual correlation with total mortality (κ)(Fig 9:1) . The symbol κ (kappa) is used to distinguish this from K, which is total mortality, including variation in natality, of the whole life cycle. Sometimes, a visual inspection of the plots of ks and K does not indicate a key factor clearly. However various methods have been developed for finding one in such situations. These include looking for a high correlation between k and K (Hassell and Huffakker 1969), a high regression coefficient of K on k (Metcalfe 1972) or vice versa (Podoler and Rogers 1975) and partitioning the variances and covariances of each of the k factors to obtain an indication of the contribution of each to the total variance (Smith 1973, Manly 1977). The latter two methods have the added benefit of not only identifying key factors but also the dependence of each on the preceding k factors. A variance/covariance matrix of the k values using the method of Smith (1973) was constructed confirm to visual findings and to assess the importance of the other mortality factors. The lack of an October sample in 1981 resulted in a combined k_2 and k_3 that year. To enable

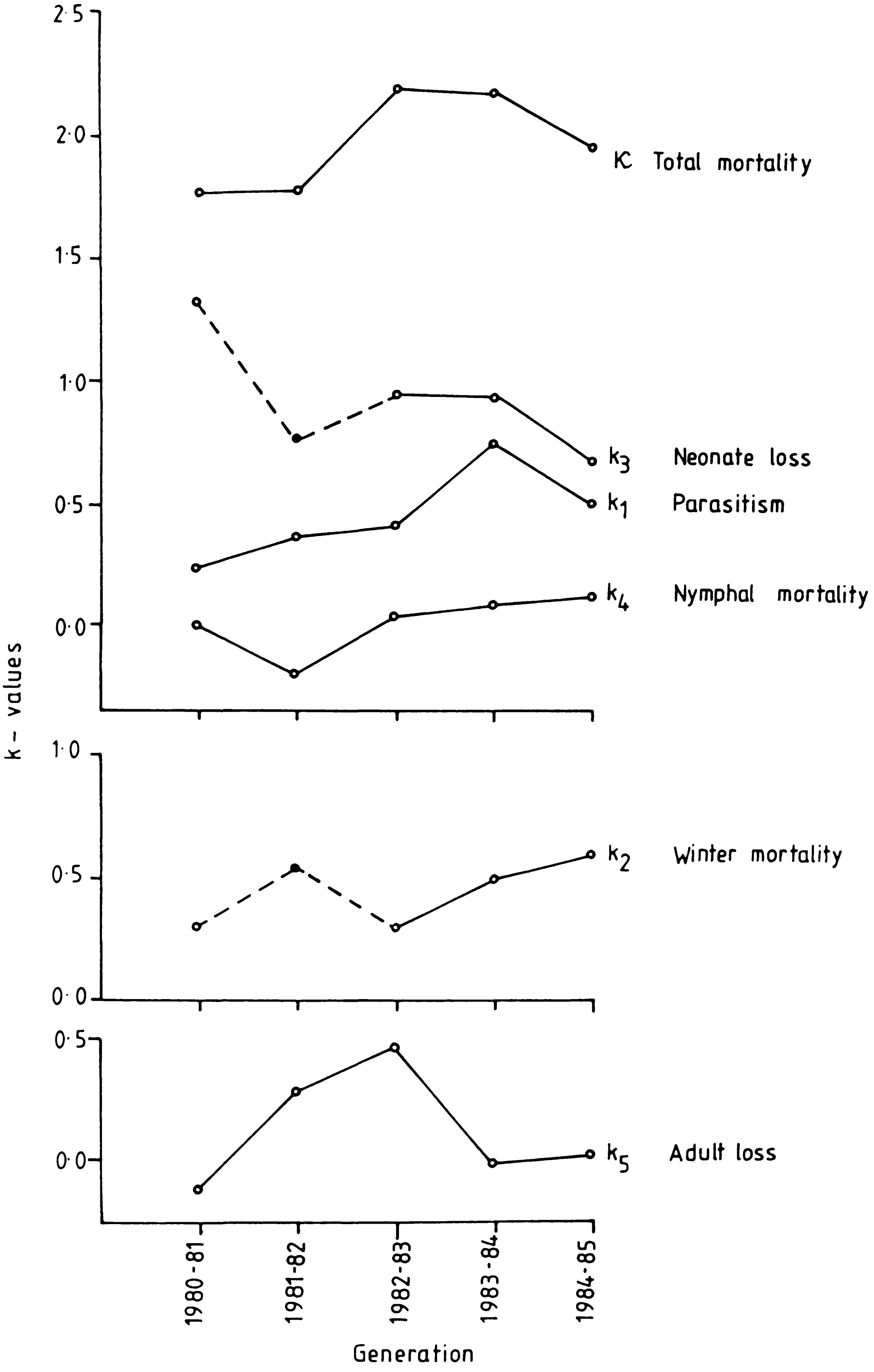


Fig 9:1 $\mathcal{K}$ and associated k values for *S. australis* population at Steele's Farm, 1980-85.

the matrix to be constructed, this figure was divided into separate k_2 and k_3 estimates using the ratio of the mean of all other k_2 values to the mean of all other k_3 values.

Field observations and egg sampling results indicated that variation in natality was important in determining *S. australis* population size from generation to generation. Although the only field estimate of fecundity was very low (43±9 in 1984), females in a suburban garden averaged 221±25 in the same year. This level of fecundity is possible in the study area since when both 1982 and 1984 egg populations are divided by half the number of adults in the preceding generation (assuming 1:1 sex ratio), the resulting figures lie within the standard errors of the suburban estimate. So that some idea of the impact of variation of natality on the population dynamics of *S. australis* could be gained, this suburban estimate was taken as an estimate of maximum fecundity. Thus k_0 (variation in natality) is the difference between possible maximum potential natality (in this case no. females x 221) and the number of eggs laid. With the above k factors, k_0 was plotted against generation so the impact on K could be assessed (Fig 9:2). Once again a variance/covariance matrix was constructed to compare the influence of k_0 to that found previously. So that the 1980-81 generation could be included, it was given a k_0 value that equaled the mean k_0 of all other generations.

The density dependence of mortality factors was tested by the method of Varley and Gradwell (1968) in which the regression of each k factor on the log density of numbers entering a stage was calculated.

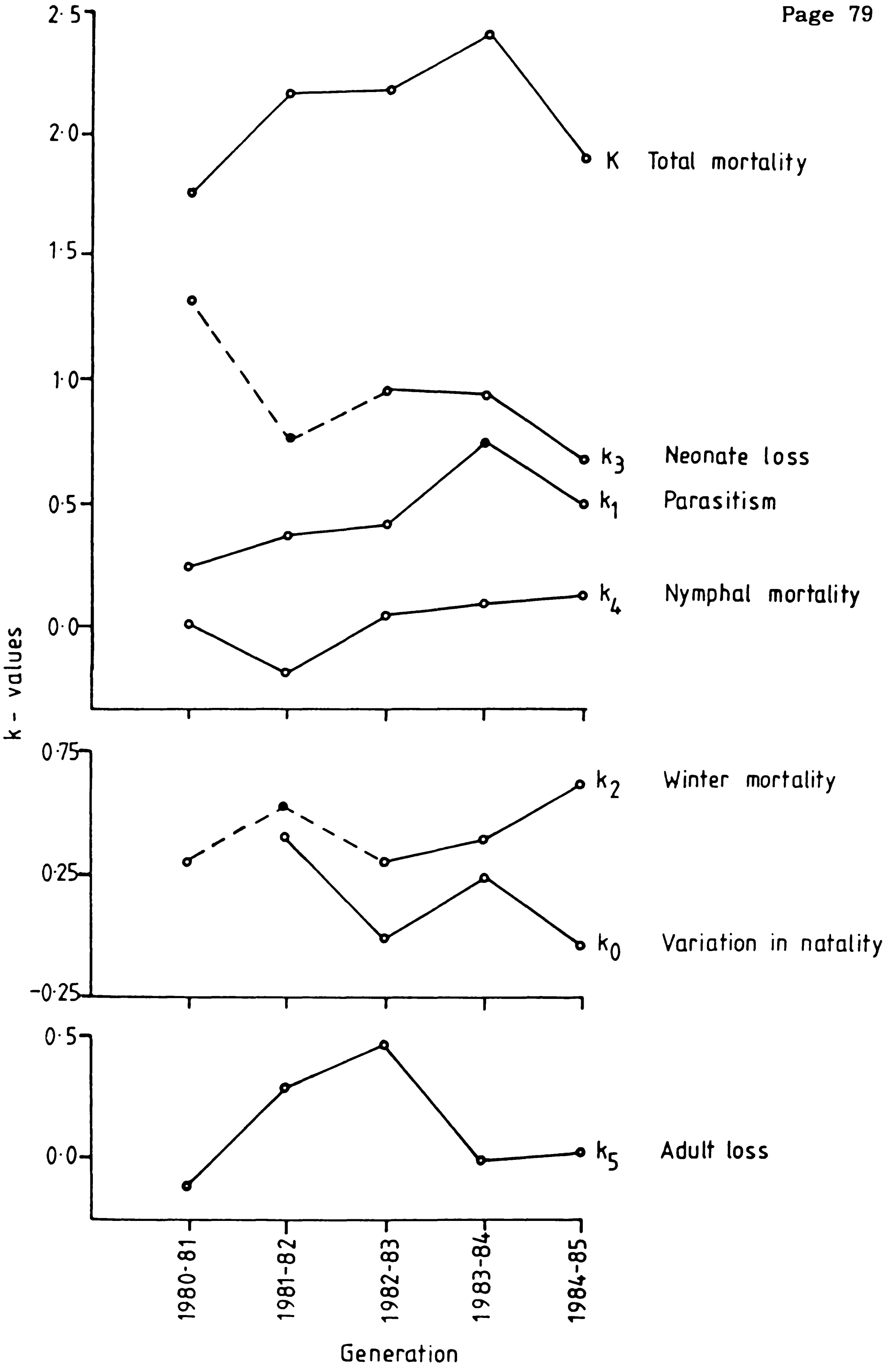


Fig 9:2 K and associated k values for the *S. australis* population at Steele's Farm, 1980-84. (N.B. no k_0 estimated 1980-81, combined 1981-82 $k_{2,3}$ divided by ratio of mean of all other k_2 values to mean of all other k_3 values).

III RESULTS

The population estimates of the 5 generations of *S. australis* in the study area are given in Table 9:2. It shows that the population is not stable, with peak numbers of eggs and nymphs occurring in the 1982-83 generation and comparatively very low numbers in the two following generations.

The k values for the 6 mortality categories were derived from Table 9:1. Visual correlation of k_1-k_5 with $\mathcal{K}$ indicates that parasitism (k_1) or neonate loss (k_3) to be the key factors and that k_3 appears to vary inversely with k_2 (Fig 9:1). Inspection of the variance/covariance matrix of the 5 values confirms parasitism as the main key factor (Table 9:3). When k_1 is taken out of $\mathcal{K}$, the next most important factor was adult loss (k_5). This tended to vary inversely with all factors, but in particular with neonate loss (k_3) which in turn was the next most important factor in determining the fluctuations in population size. Neonate loss was the largest mortality and was inversely dependent on k_2 (winter mortality) and possibly k_1. Both k_2 and k_4 (nymphal mortality) were minor factors, with k_4 being directly dependent on k_1.

When k_0 (variation in natality) is included and all the k factors, along with total K, are plotted against generation, k_1 is still the main key factor (Fig 9:2). Visually k_0 varies inversely with k_5. The variance/covariance matrix of all 6 k values once again confirmed parasitism as the key factor (Table 9:4). When the effect of k_1 is subtracted, k_0, k_4 and k_5 all then become the next most important predictive factors. Parasitism is independent of k_0. When compared with the previous matrix (Table 9:3), k_2 remains a minor factor, independent of all others. Neonate loss (k_3) is still inversely

Table 9:2 Census data of *S. australis* in gully site over 5 generations: Populations expressed as no./m^2

stage	1980-81	1981-82	1982-83	1983-84	1984-85
Potential eggs*		28620	22321	17128	5857
Eggs laid	15120	11280	21400	8429	6501
Eggs surviving parasitism	8640	4740	7894	1465	2004
Eggs surviving winter	4320	-	3987	588	487
Early instars	204	234	435	65	99
Late instars	200	357	381	51	70
Adults	259	188	132	53	68

* Using suburban 1984 fecundity estimate of 221

Table 9:3 Variance/covariance matrix for k values (excluding k_0) and the total $\mathcal{K}$.

	k_1	k_2	k_3	k_4	k_5	$\mathcal{K}$
k_1	·030					
k_2	·004	·019				
k_3	-·016	-·023	·048			
k_4	·010	-·001	-·002	·013		
k_5	-·004	-·003	-·017	-·009	·045	
$\mathcal{K}$	·024	-·006	-·009	·014	·013	·047

Table 9:4 Variance/covariance matrix for k values and total K

	k_0	k_1	k_2	k_3	k_4	k_5	K
k_0	·027						
k_1	·000	·030					
k_2	·002	·004	·016				
k_3	·000	-·016	-·023	·048			
k_4	-·015	·010	·003	·000	·013		
k_5	-·001	-·004	-·003	-·017	-·009	·045	
K	·014	·025	-·004	-·007	-·001	·012	·047

dependent on k_1 and k_1 but not on k_0. Nymphal mortality (k_4) remains directly dependent on k_1 and is inversely dependent on k_0. In the second matrix, k_5 varies inversely with all other factors, especially k_3.

The various k factors were plotted against the log of density of numbers entering the stage on which the mortality factor acted and the results are presented in Fig 9:3. Only k_5, k_3, k_2 and k_0 had possible density dependent relationships but with the few generations studied, the regressions were not significant at the 5% level, the closest being k_1 with $0{\cdot}1<P<0{\cdot}05$ (k_0 $t=1{\cdot}28$, k_1 $t=2{\cdot}55$, k_2 $t=1{\cdot}39$, k_3 $t=1{\cdot}61$, k_4 $t=0{\cdot}61$, k_5 $t=1{\cdot}71$). Parasitism may be a delayed density dependent factor, as indicated by the anticlockwise cycling when the points from the consecutive years are joined (Fig 9:3).

IV DISCUSSION

Life tables for consecutive generations of *S. australis* have not previously been published. Population studies on grassland Auchenorrhyncha fauna have been reviewed by Waloff (1980), who identified eggs as the most vulnerable stage of all species studied intensively. Reproductive failure (k_0) and egg mortality (k_1) were not always distinguished but the key factor lay in the combination of both. Egg parasitism, principally by *Anagrus* spp. (Mymaridae:Hymenoptera) caused up to 44% mortality. Fungal attack was found to be a key factor in *Cicadella viridis* (Cicadellinae). Nymphal mortality, although often very high, was not identified as a key factor and did not have a definite regulatory role in any of the species examined. Small scale migrations and frequent changes of breeding sites were said to appear to be characteristic of a number of species of Auchenorrhyncha.

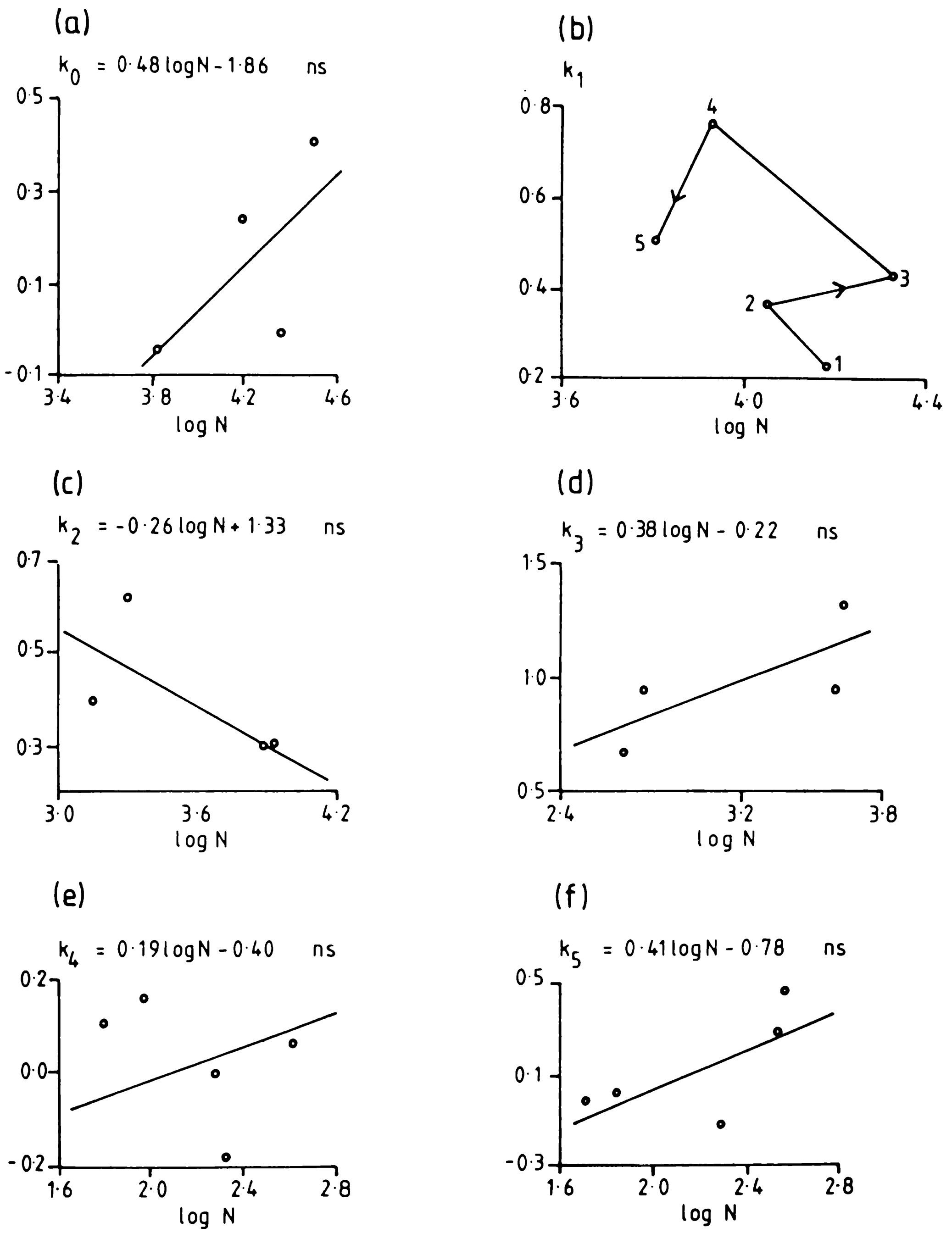


Fig 9:3 Plots of k values against the log densities of *S. australis* on which they acted: (a) k_0, variation in natality; (b) k_1, parasitism mortality, 1-5 are successive generations; (c) k_2, winter mortality: (d) k_3, neonate loss; (e) k_4, nymphal mortality: (f) k_5, adult loss. (ns = not significant).

Life table analysis of the blackberry leafhopper *Dikrella californica* Lawson demonstrated density dependent mortality to an *Anagrus* egg parasite (Williams 1984). However , Metcalfe (1972) in his study on the population dynamics of *Saccharosydne saccharivora* Westw. (Homoptera:Delphacidae), found that the key factor was mortality between instar 1 and reproducing adults or between peak instars 3-5 and reproducing adults. The key factor was density independent and of all the factors within it, adult dispersal was considered the most important.

As in the grassland Auchenorrhncha leafhoppers (Waloff 1980) the egg mortality of *S. australis* contained the key factor. The dominant influence of parasitism by *C. scolypopae* on the population trend was not anticipated as it was thought parasitism levels may not have been sufficiently high. The apparent absence of any strong density dependent factors involved in limiting *S. australis* numbers could be the explanation since early mortality in a host egg stage can be negated by density dependent mechanisms in later stages. This has been considered one reason for the poor record of *Trichogramma* spp. (Hymenoptera,Trichogrammatidae) as biological control agents against graminaceous stalkborers in general (Hassell and Waage 1984).

The anticlockwise cycling of k_1 in Fig 9:3 is suggestive of a delayed density dependent relationship between host and the parasite. *C. scolypopae* do not emerge until hopper oviposition has commenced and are not affected by mortality factors such as deleterious climatic conditions that may act on the host population over the spring and early summer. The parasite abundance is determined largely by the size of the previous host generation. Thus, when host egg numbers dropped dramatically in 1983, compared with 1982 levels (Fig 5:6), mortality by parasitism reached very high levels for the 1983-84 generation (Fig

9:1). The effect of the high parasitism levels flowed into the following generation since the host adult population was so low. Even with a high production of eggs/adult (Table 9:2), parasitism was still high in 1984, although less than 1983. However, with maximum host fecundity being approximately 5 times greater than that of *Centrodora scolypopae*, favourable seasons would see the host returning to former population levels before the parasite. The irregularity of Fig 9:3 suggests that other processes were interacting with parasitism. Host plant affects parasitism levels and small changes in *S. australis* egg distribution would give changes in percent parasitism thus giving rise to irregularities in the relationship.

The second most important k factor in determining population size was variation in natality (k_0)(Fig 9:2), although the lack of fecundity data means that any conclusions drawn from the k factor analysis are tentative. Also, the possibility of adult migration, which was not studied, means that the estimate of adults present at peak oviposition time may not represent the number of adults ovipositing in the area. Although assumptions were made in assessing the actual levels of population fecundity, errors in estimating the value would only alter the magnitude, not the existence of the observed fluctuations in k_0. The peak k_0 value for the 1983-84 generation coincides with a cold summer in the 1982-83 season. The cumulative day degrees calculated from Rukuhia data over December, January and February that year totaled 378 °D, compared with 531 in 1980-81, 506 in 1981-82 and 439 in 1983-84. These temperatures slowed hopper development, delayed adult appearance and reduced the time available for oviposition. It is considered that the large drop in egg numbers and the resulting high k_0 was caused by the reduced fecundity of the *S. australis* females that year (Chapter 7). Similar results were found by Whittaker (1971, 1973) in populations of *Philaenus spumarius* (Homoptera:Cercopidae) and *Neophilaenus lineatus* (Homoptera:Cercopidae), where large changes in density from one generation to the next were caused by differing weather conditions at the end of the season when oviposition took place. One or more batches of eggs were laid, depending on the season. Reduced fecundity was an important factor in *Pyrilla perpusilla* (Homoptera : Lophopidae) populations although in this case a parasite, as well as low temperatures, was responsible (Brar and Bains 1979). In the present study, no overall relationship was found between cumulative day degrees each year and the respective k_0 values so it is likely that other factors are involved, such as host plant vigour, which could be affected by rainfall and amount of sunshine.

Adult loss (k_5) was the second most important predictive factor in Fig 9:1 and was second equal when k_0 was included (Fig 9:2). Both adult mortality and migration are included in this estimate and cannot be separated with the information available although the negative k_5 values indicate inward migration of outside females. The inverse relationship of k_5 with other k factors in the variance/covariance matrix (Table 9:4) indicates that k_5 has a smoothing effect on the population with greatest losses occurring in years with low mortality and loss from other k factors and indicates a density dependent action. The apparent inverse relationship with k_0 in Fig 9:2 indicates that low adult mortality occurs when conditions favour optimal fecundity in females, resulting in a low k_0 value in the next generation.

The life table and k factor analysis of the data demonstrated that the time of largest loss of individuals within a generation was at the neonate nymphal stage (k_3). This loss could result from several factors, such as failure to emerge from the egg, failure to find suitable host plants, susceptibility to adverse environmental conditions at the time, and differences arising from the precision of the absolute egg estimates and the comparative relativity of the nymphal estimates. Failure to emerge from the egg is a minor factor as very few unhatched eggs are found once emergence is complete. Nymphal sampling deficiencies would not account for such large losses, even if the true population was double that observed. It is considered that failure to find a host plant is the major factor. Neonate nymphs often emerge quite some distance from current season's growth. Within enclosed containers in the laboratory, newly emerged nymphs demonstrate positive phototaxis and negative geotaxis. They move predominantly by walking and many die, failing to find the host plant provided a few centimetres away from where they were released. In the field, due to the greater distances and the added influence of deleterious weather and environmental conditions, losses are bound to be high. No predators of this stage were detected but their small size may well have a bearing on this observation. Although the largest mortality factor, neonate loss was not a key factor and its action was independent of population density (Fig 9:3) and other prior mortality factors (Tables 9:3-4). This is a similar finding to that in grassland Auchenorrhyncha species (Waloff and Thompson 1980, Waloff 1980).

Both winter mortality (k_2) and nymphal mortality (k_4) were very small compared with other factors (Fig 9:1). Winter mortality includes parasites killed by fungi as it was impossible to decipher the initial cause of mortality in most cases. The inability to distinguish the factor responsible for causing the death of the host is discussed by Royama (1981) who developed the concept of 'killing power' of a mortality factor which then could be incorporated into a model of the effect any given factor would have on the dynamics of the population concerned. As it was a portion of parasitism mortality that was being masked and this was already determined as the key factor in the population dynamics of *S. australis*, further manipulation of the data was not considered warranted.

V CONCLUSIONS

From the analysis of the life tables, it has been found that parasitism by *C. scolypopae* is the key mortality factor in the population dynamics of *S. australis* and is likely to have a delayed density dependent relationship with the host population. No other density dependent mortality factors were proved although adult loss has a possible interaction with previous mortality factors. Neonate loss accounted for the highest proportion of *S. australis* mortality but had no definite regulatory role. Nymphal mortality was the smallest mortality factor and showed no signs of density dependence, as was found by Whittaker (1973) in his study of *N. lineatus*. Advocates for the introduction of exotic biological control agents may do well to search for predators, parasites or microbial organisms that may be more effective against this stage which appears almost untouched by those which already exist. Overseas fulgoroid nymphs are known to be attacked by ectoparasites (Waloff 1980, Swaminathan and Ananthalcrishnan 1982), endoparasites (Stiling and Strong 1982, Waloff 1980), nematodes (Kuno 1984, Swaminathan and Ananthalcrishnan 1982), entomogenous fungi (Varma et al. 1977, Barbosa et al. 1979) and a range of predators (Barbosa et al. 1979, Kuno 1984, Waloff 1980, Swaminathan and Ananthalcrishnan 1982). Nymphal and adult parasitism by *Stenocranophilus quadratus* Pierce (Strepsiptera:Halictophagidae) was a very important mortality factor in the population dynamics of *S. saccharivora* (Metcalfe 1972).

The key role that *C. scolypopae* plays in determining the size of

S. australis populations makes it a worthy subject for further study of its biology and interaction with its host. The interaction of only a single parasite and host is not common in nature (Hassell and Waage 1984) and study of one such as this aids the understanding of the more complex multi-species interactions.

SECTION D

BIOLOGY, MORPHOLOGY AND POPULATION ECOLOGY OF CENTRODORA SCOLYPOPAE

CHAPTER TEN

BIOLOGY AND MORPHOLOGY OF CENTRODORA SCOLYPOPAE

I INTRODUCTION

The genus *Centrodora* consists of 29 known species (Hayat 1974, 1981). They are minute, yellow or pale coloured parasites. Definite host records are known for 16 species only (Hayat 1974). All are parasitic on eggs (often in woody tissue) of orthopterous and homopterous insects, with the exception of *C. speciosissima* which parasitises pupae of dipterous, chalcid and proctotrupid insects.

Although there is a intergradation with other genera, particularly *Aphytis* (Howard) and *Tumidiscapus* (Girault), *Centrodora* (Foerster) can be separated on morphological and biological grounds (Valentine 1966). The systematic position of *Centrodora* as determined by Yasnosh (1976) is given below;

Order:Hymenoptera
Suborder:Aprocrita
Superfamily:Chalcidoidea
Family:Aphelinidae
Tribe:Centrodorini
Genus:Centrodora

The species *Centrodora scolypopae* was first found in *Scolypopa australis* eggs in the Bay of Islands, N.Z. in 1962 (Cumber 1966). It was identified as a new species and the adult external morphology described by Valentine (1966). The females are 0•9-1•1 mm in length and a dull dusky yellow colour with a darker brown pattern on the thorax and margins of the abdomen (Plate 10:1). The abdomen is elongate with the ovipositor extruded. The males are usually much smaller than females (0•5-0•7 mm) and yellow in colour without any distinct pattern. The abdomen is only a little longer than the thorax (Plate 10:2).

Cumber (1966) observed several biological features of *C. scolypopae*. Host eggs nourished 1-4 individuals although 2, one of each sex, was most common. The sex ratio at emergence favoured females, 2:1. Parasitised eggs were readily distinguished by a general darkening, a transverse dark band and a dark spot at the point of ovipositor insertion. He observed a period of arrested development that synchronised adult emergence with the new season's hopper eggs. Also, parasitism of *Scolypopa* eggs decreased from North to South and varied with the host plant, with highest parasitism on *Pteridium* spp. compared to other species.

The present study offered a unique opportunity to study the biology of a representative of the genus *Centrodora*. Most Aphelinids are primary parasites of the sternorrhynchous Homoptera (Aphidoidea, Aleyrodoidea and Coccoidea) and much is known about the biology of the genera *Coccophagus*, *Encarsia* and *Aphytis* which are of considerable economic importance for biological control (Viggiani 1984). *Centrodora* are specialised egg parasites and little is known of their biology since, apart from *C. scolypopae* and *C. coocata*, which is a parasite of a cicadellid forestry pest of wattle trees (Annecke and Insley 1972), the genus has not yet been of much importance for biological control.

II MATERIALS AND METHOD

Parasitised *Scolypopa australis* eggs were readily obtainable from the Steele's farm site for most of the year. Adults were obtained by

Plate 10:1 Male *C. scolypopae* adult (slide mounted specimen, bright field, mag. 100×).

Plate 10:2 Female *C. scolypopae* adult (slide mounted specimen, bright field, mag 100×).

rearing them from field-collected host eggs in the laboratory. The most convenient method was to place the parasitised oviposition material in "growth" jars and holding at a temperature of 20-25°C. Each jar consisted of an "Agee" jar containing water in the base with the oviposition material held above on a gauze mat supported by plastic pipe (see Fig 10:1). The jars were closed with an "Agee" seal and ring. Each seal had a hole punched in the centre in which a rubber bung was fitted. When adults were about to emerge, the solid bung was replaced with a hollow one pushed up through from the inside. A test-tube could then be fitted to the bung in an inverted upright position (Fig 10:1). The jar was placed in a box, covered so only the test tube protruded, then placed where the tube was exposed to light. *Centrodora* adults show strong positive phototaxis and negative geotaxis and so readily collected in the test tube end. When test tubes contained adults, they were removed from the growth jars and replaced with fresh tubes.

C. scolypopae females oviposited readily when in test tubes. Fresh *Scolypopa* oviposition material was collected from a home garden in Hamilton where *C. scolypopae* numbers were low. Raspberry was the main host plant used because almost no parasitism was found on it naturally, possibly because annual pruning prevented any carryover from previous generations. Also host eggs were relatively free from disease and mites so parasites could be reared with few losses.

Because adults usually died within 24 hours when not fed, a fine streak of honey was usually placed in each test tube. Oviposition material was placed in with the adults and the tubes closed with a bung. Oviposition usually commenced within minutes and the host material was left with the adults till the following day when it was replaced with fresh material.

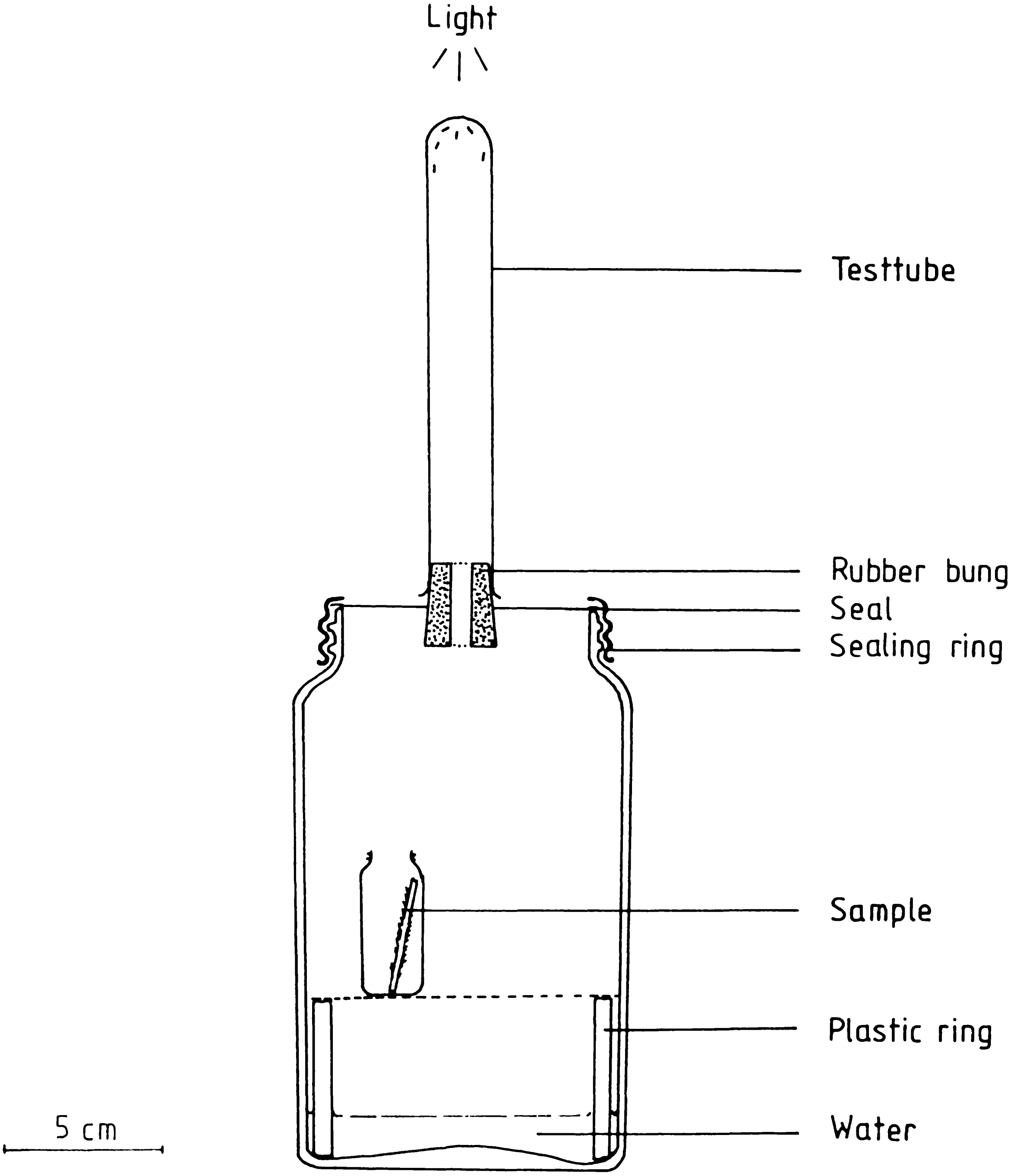


Fig 10:1 Apparatus used in the rearing and collection of *C. scolypopae*.

The parasitised host material was then put into unsealed labelled glass vials and stood on a gauze mat over water (Fig 10:1). Desication was thus avoided although fungal growth caused by the high humidity was a minor problem.

The developmental stages of *C. scolypopae* were ascertained with the use of a microscope by dissecting out the parasitised eggs from the woody oviposition material. The parasitised eggs were immersed in 70% ethanol which cleared the host egg cuticle and made the parasite easily visible in most cases. Closer examination of the parasite was obtained by dissecting the host egg in insect Ringer's solution. Live material was often mounted in Ringer's solution for study under high power. Permanent slide mounts were prepared by putting eggs and first instar larvae directly into a drop of Hoyer's medium on a glass slide and covering with a coverslip. Larger larvae were punctured with an entomological pin first to eliminate the opaque gut content.

Scanning electron micrographs (SEM) were taken on a JEOL-JSM 35 at 25KV. Pupae were prepared washing in a KH_2PO_4/Na_2HPO_4 buffer, fixing in 4% gluteraldehyde and buffer then dehydrating in an ethanol series. They were then critical point dried in CO_2, then coated with 500 A° Au/Pd in a diode sputter coater.

Dissection of adults to examine internal genitalia was difficult because of the small size and was done in a drop of water or Ringer's solution on a glass slide under a binocular stereomicroscope.

III MORPHOLOGY

1, Developmental stages

The deposited egg and three larval instars of *C. scolypopae* are shown in Plate 10:3.

a, Eggs

The deposited *C. scolypopae* egg is 270 microns long and 50 microns wide, has a transparent, unsculptured chorion and is stalked with a distinct border separating the egg proper from the stalk (Fig 10:2a). Incubation takes 8-10 days at room temperature and there is no change in size during this time. The yolk of the host egg becomes clearer during parasite egg incubation and the parasite eggs sink to the lowest portion of the host egg indicating the breakdown of yolk structure by parasitic enzymes. It is possible that these come from the parasite female during oviposition as the clearing still occurs when parasite eggs fail to hatch (e.g. at 10°C) and in the very rare host egg bearing an parasite oviposition scar but containing no parasite.

Stalked eggs are common in the parasitic Hymenoptera. In the Aphelinidae they occur in the genera *Aphytis*, *Marietta* and *Centrodora*, which are closely related, and also in *Aspidiotiphagus* (Hagen 1964). They are often associated with Hymenoptera with long ovipositors, the extension permitting the egg to be compressed and stretched while passing down the ovipositor (Hagen 1964).

b, Larvae

All aphelinid genera apparently have three larval instars (Nikol'skaya and Yasnosh 1966) and *C. scolypopae* does not differ. The three instars differ in mandible shape and in amount of morphological differentiation.

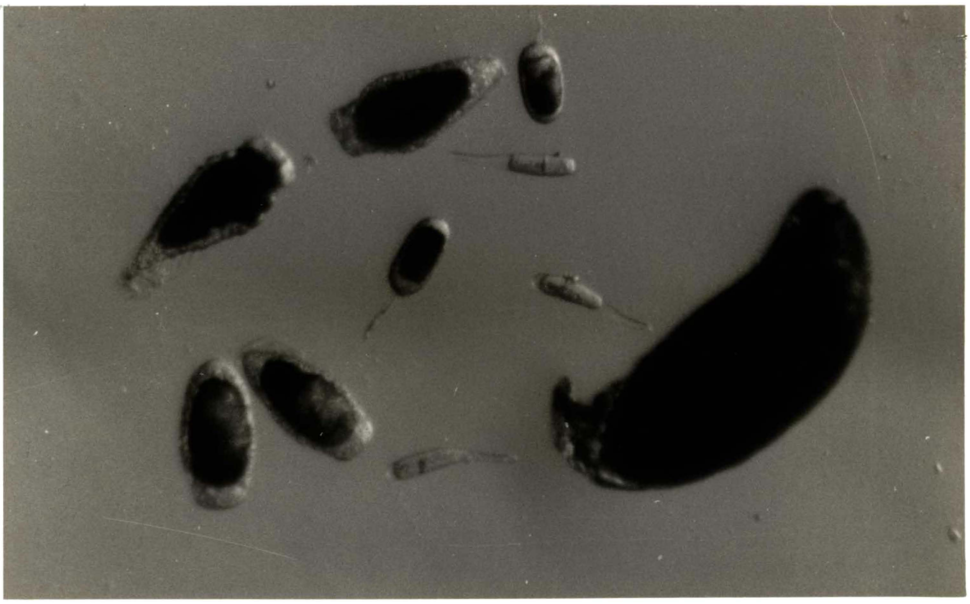
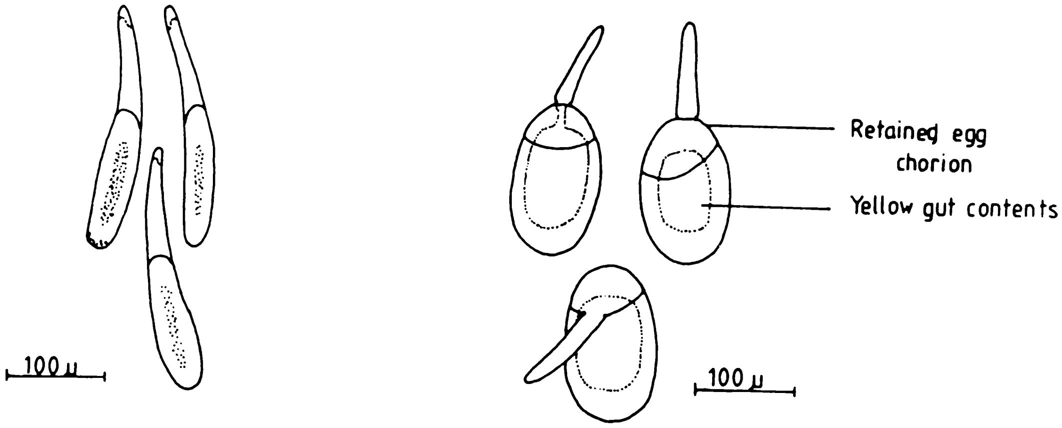
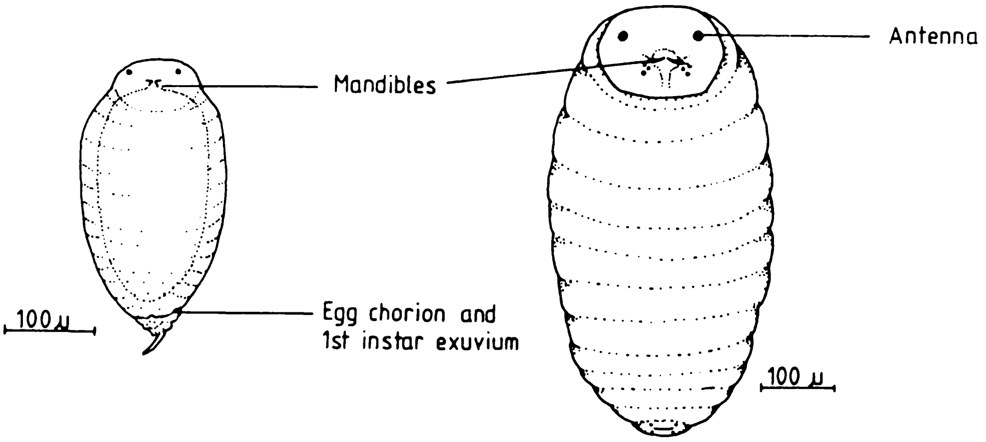


Plate 10:3 Deposited eggs and larval instars of *C. scolypopae*.
(Mature 3rd instar out of focus). 60 x



(a) Egg (b) 1st instar



(c) 2nd instar (d) 3rd instar

Fig 10:2 Egg and larval stages of *C. scolypopae*.

i. First instar

The newly hatched larva is ovoid, measuring 150-175 μ in length. No segmentation or mouthparts are visible. The gut is visible as a light yellow barrel shape in the centre of the larva. The anterior of the larvae remains within the egg chorion (Fig 10:2b). This retention of the egg chorion also occurs in the Encyrtidae where it is thought to play a role in respiration (Maple 1947). No tracheal system or spiracles were observed. All families that are predominantly egg parasites (Mymaridae, Trichogrammitidae and Scelonidae) have first instar larvae that respire through the integument and lack spiracles (ie are apneustic) (Hagen 1964). The lack of morphological structures in the first instar of *C. scolypopae* compared to aphelinids, such as *Aphytis chilensis* (Howard), which has 4 pairs of spiracles and a readily visible cephalic skeleton (Rosen and Eliraz 1978), indicates a specialised adaption to life as an egg parasite.

ii. Second instar

The second instar, measuring 266±10 μ in length (range 250-325 n=10), shows slight differentiation. The barely discernable cephalic skeleton has transparent triangular mandibles (Fig 10:3, Plate 10:4). The thoracic and abdominal segments are faintly visible. The first instar exuviae and egg chorion remain loosely attached to the last segments (Fig 10:2c). Male and female larvae within each host egg can be distinguished by their size, the male growing at a slower rate than the female (Plate 10:5).

iii. Third instar.

This is the last instar and has clear segmentation with the head and 13 body segments clearly demarcated. The gut is opaque white and

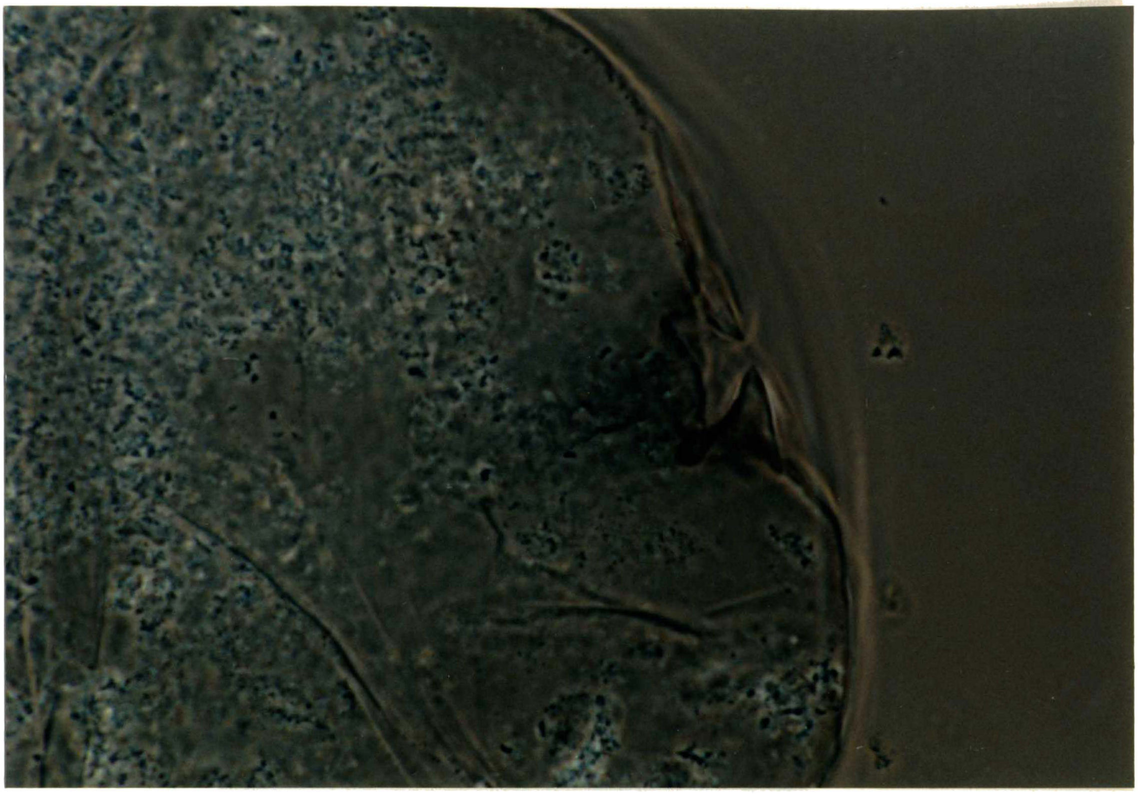


Plate 10:4 Mouthparts of 2nd instar *C. scolypopae* larvae, (positive phase contrast, mag 1250x).

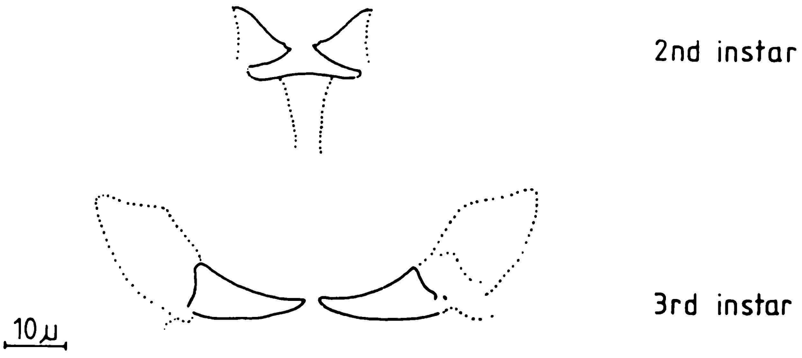


Fig 10:3 Mandibles of *C. scolypopae* larvae.

Plate 10:5 Male and female 2nd instar *C. scolypopae* larvae from single oviposition. 150x

occupies most of the body cavity. Initially the body segments taper sharply but the larvae quickly become oval in shape when viewed dorsally. The ventral surface is flat or slightly concave, the dorsal surface convex. Maximum size of the female is determined by the *S. australis* egg dimensions (845±5 μ long 400 μ wide). Males average 385±35 μ long and 181±31 μ wide.

The cephalic skeleton (Plate 10:6) is typical of the chalcidoids with little differentiation, the mandibles being the main discernible parts. The epistomal, pleurostomal, hypostomal and tentorial sclerites form a continuous ring. The mandibles are smooth, tapering and gently curved (Fig 10:3). The pharynx opens between the mandibles. The one segmented antennae are disc-like structures in the middle of circular antennal sockets. There are 4 circular structures, with a possible sensory function, and 2 cuticular protruberences on either side of the mandibles (Plate 10:7).

Pairs of spiracles are found on the mesothoracic and second, third and seventh abdominal segments (Plate 10:8, Fig. 10:4). Mature chalcidoidea larvae usually have 9 open spiracles but the larvae of the egg parasites Mymaridae and Trichogrammatidae (the latter being closely related to Aphelinidae) never develop a trachael system (Fisher 1971). The reduction in the number of spiracles in mature *C. scolypopae* larvae and the complete lack in the earlier instars is presumably an adaption to the existence as a egg parasite.

iv. Prepupae

The prepupal stage of the third instar can be divided into two phases similar to those described by Hagen (1964). The eonymphal phase begins when the third instar ceases to feed. Usually the larvae assume

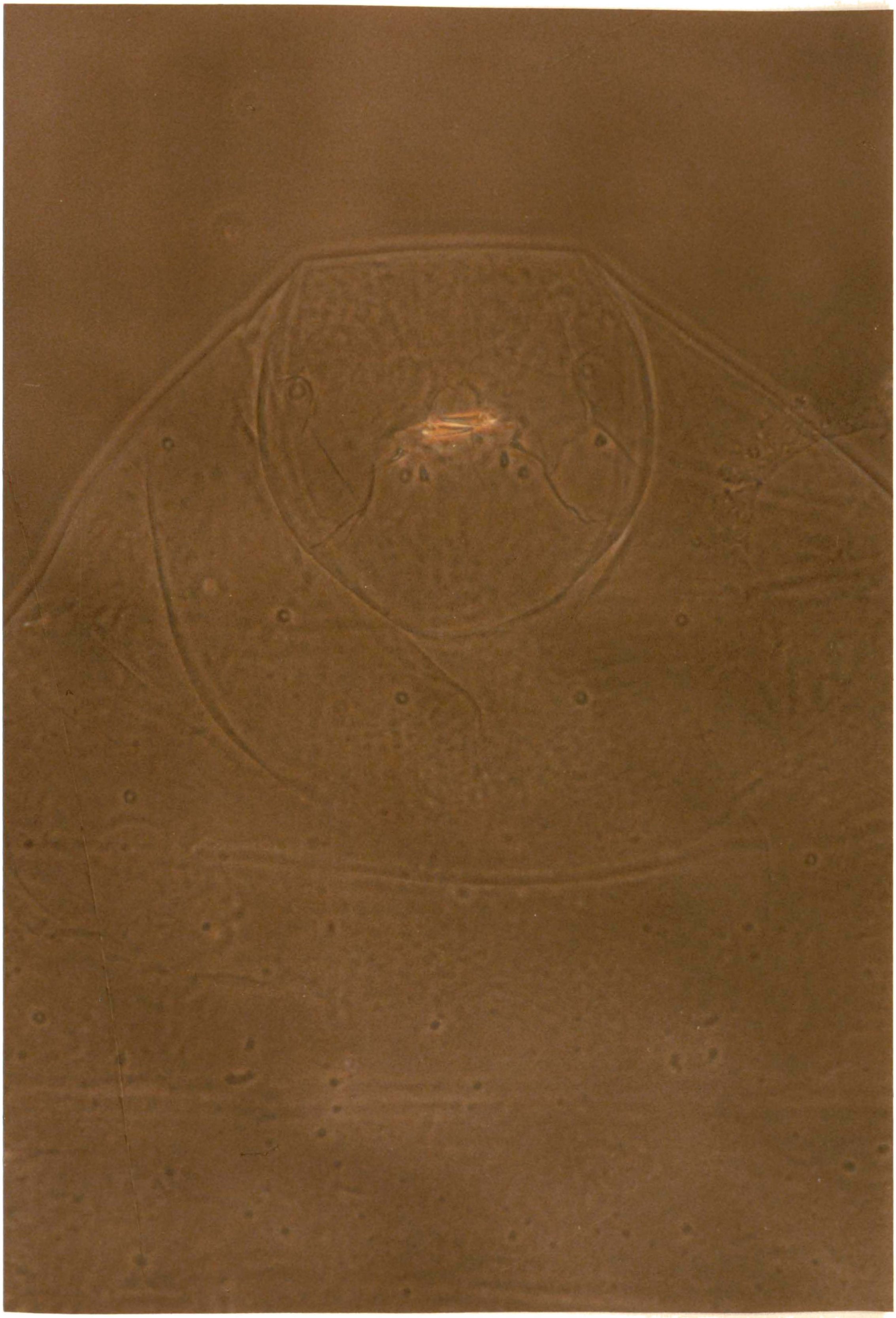


Plate 10:6 Anterior of 3rd instar larva showing cephalic skeleton (mag 320×).

Plate 10:7 Antennae and mouthparts of 3rd instar larvae (D.I.C. mag. 1250×).

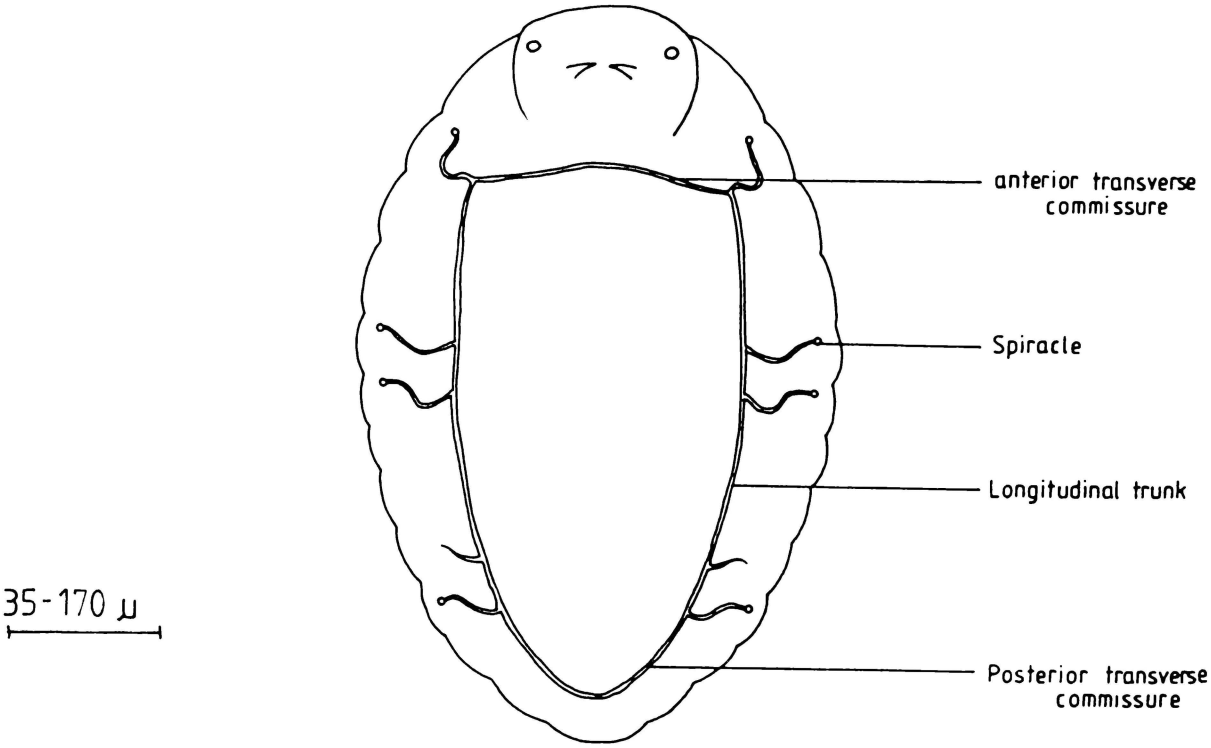


Fig 10:4 Respiratory system of 3rd instar *C. scolypopae* larva.

Plate 10:8 Cuticle of 3rd instar larvae showing 4 pairs of spiracles (positive phase contrast 100×).

a head-down position with the male, if present, at the base, furthest away from the micropyle. A dark grey bar, visible from the outside, appears at the ventral surface. This is in a double layered membrane, which is part of the *Scolypopa* egg as the puncture made by the *C. scolypopae* female is easily visible in it, often with grey pigmentation surrounding it also. The appearance of the bar is also accompanied with an increase in egg size. Host eggs containing mature parasite larvae average 845+5 μ (n=50) while barred eggs average 933±6 μ (n=82) in length. The larval cuticle is more transparent and the gut shrinks and becomes more dense. The larvae overwinter in this stage which lasts 8-9 months in the Hamilton area. However at a constant temperature of 20°C or above with a long day light regime, (ie in the absence of diapause), this phase takes about 7 days.

The second or pronymphal phase of the prepupal stage is marked by the excretion of faecal material, in the form of 4-6 orange meconial pellets which lie neatly alongside the abdomen. Differentiation of the pupal structures is rapid.

v. Pupa

The pupa is exarate. The female averages 858±73 μ and the male 579±19 μ. The female lies on the ventral side of the host egg with her head near the micropyle facing upwards. The male lies facing the female at the base of the egg (Fig 10:5a). The ventral aspect of the pupa is depicted in Fig 10:5b. Antennal cases are present on each side of the head. Below these are the mouthpart cases: the labrum is absent, the mandibles triangular; the pupal maxillae have two segments and the labium has three. The prosternum and mesosternum are large bilobed plates but the metasternum is formed by two separate triangular

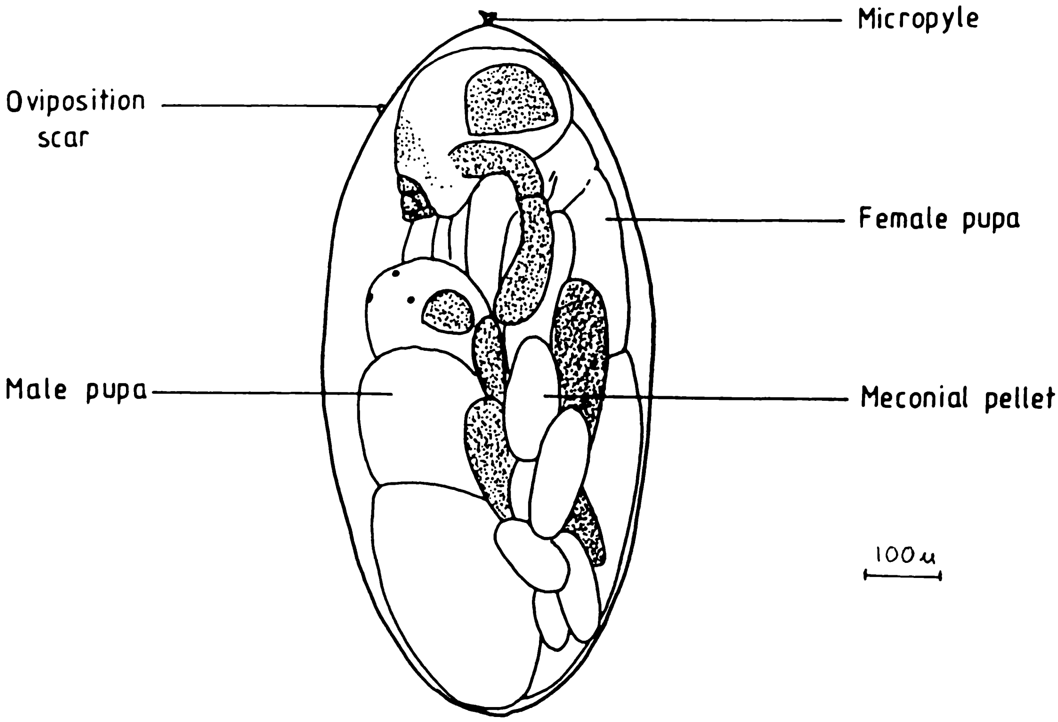


Fig 10:5a Male and female *C. scolypopae* pupa within host egg.

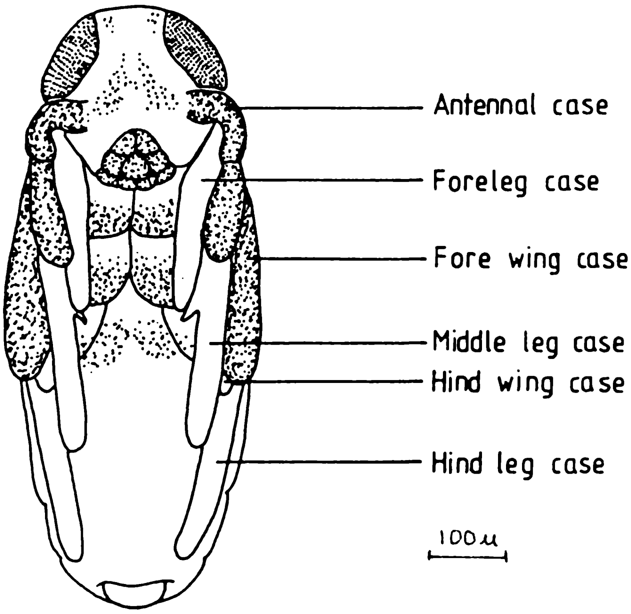


Fig 10:5b Female *C. scolypopae* pupa, ventral view.

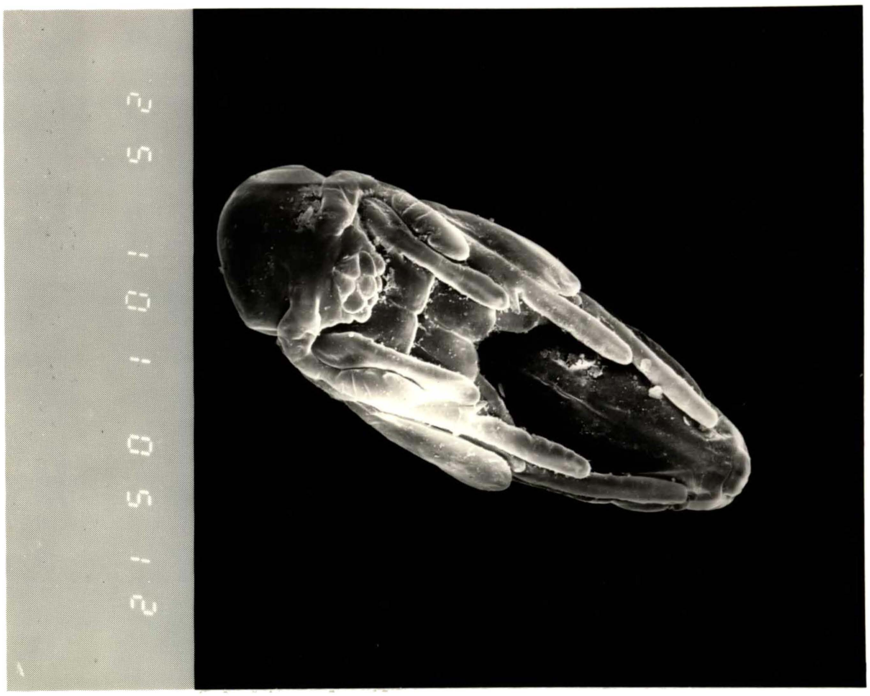


Plate 10:9 SEM of ventral view of female *C. scolypopae* pupa. 101x

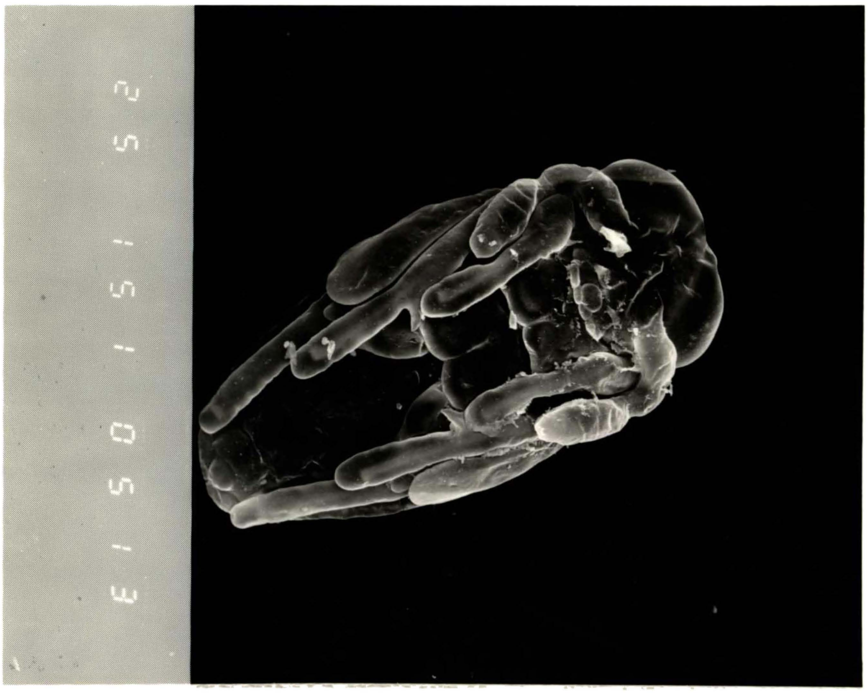


Plate 10:10 SEM of ventral view of male *C. scolypopae* pupa. 151x

plates. The forelegs are above and adjacent to the antennal cases posterior to which are the cases of the mid and hind legs. A triangular process on the mid leg cases marks the site of the prospective mid-tibial spur. The forewing cases and tip of the hind wing cases can be seen to the side between the mid and hind leg case. The antennal cases, mouthparts and leg and wing cases become pigmented a dark grey. The eyes change from colourless to grey, then to dark red.

Eclosion occurs within the host egg. The pupal integument splits and moves to the lateral sides of the parasite. The adults do not emerge immediately but remain within the egg chorion until the female's eggs are mature. Hymenoptera which reach the adult stage with their full complement of ripe eggs and do not develop further eggs during life are called proovigenic (Flanders 1950). The eggs are produced from stored nutrients. The female then chews around the uppermost portion of the egg and pushes through the frass formed by the host when ovipositing. The male, if present, follows through the same exit hole.

2, Adult reproductive morphology

a, Female reproductive system

i, Internal morphology

The female internal reproductive system (Fig 10.6) consists of a pair of ovaries opening into right and left oviducts which in turn form a common oviduct. There is a pair of collaterial glands opening dorsolaterally into the common oviduct and a spermatheca whose duct enters ventrally beneath the union of the single oviducts. An acid gland with associated reservoirs and an alkaline gland open into the vagina just above the bulbous articulation.

In common with Chalcidoidea, the ovaries each comprise of 3 ovarioles as found by Copland (1976) and Iwata (1962). The number of mature eggs per ovariole was usually from 4-6. The ovarian eggs, which lie alongside each other close to the oviduct are identical in shape to the deposited egg, unlike many Encyrtidae and some Apelinidae, such as *Aphytis chilensis*, which have a double bodied ovarian egg and a deposited egg with a narrow stalk (Rosen and Eliraz 1978).

The collaterial glands are of typical aphelinid shape, globular and relatively large. They contain a milky white substance of fibrous nature. The spermatheca (Fig 9:7) also is similar to that in other chalcid families consisting of a terminal capsule in which sperm are stored, a gland and a duct. It is bright yellow as in all other Aphelinid families reported (Copland 1976). The duct has an S bend beneath the capsule, surrounded by muscle. Copland (1976) suggested that this section was a valve to enable sperm to enter or leave the capsule.

The alkaline gland is present throughout Hymenoptera. It consists of a tubular gland of glassy appearance and a long narrow duct, as in other chalcids. It contains a viscous material which in *N. vitripennis* was shown to be a protein-carbohydrate complex with a possible lubricatory role (King and Ratcliff 1969). In some Braconid this gland produces a substance that results in host discrimination (Vinson and Guillot 1972). Many Aphelinidae are known to be good at avoiding previously parasitised host (Clausen 1940), and Copland (1976) linked this ability in *Aphelinus* spp. with their relatively large alkaline glands. Comparitively the alkaline gland of *C. scolypopae* is not so well developed.

The acid gland differs from that typical to Aphelinidae. The

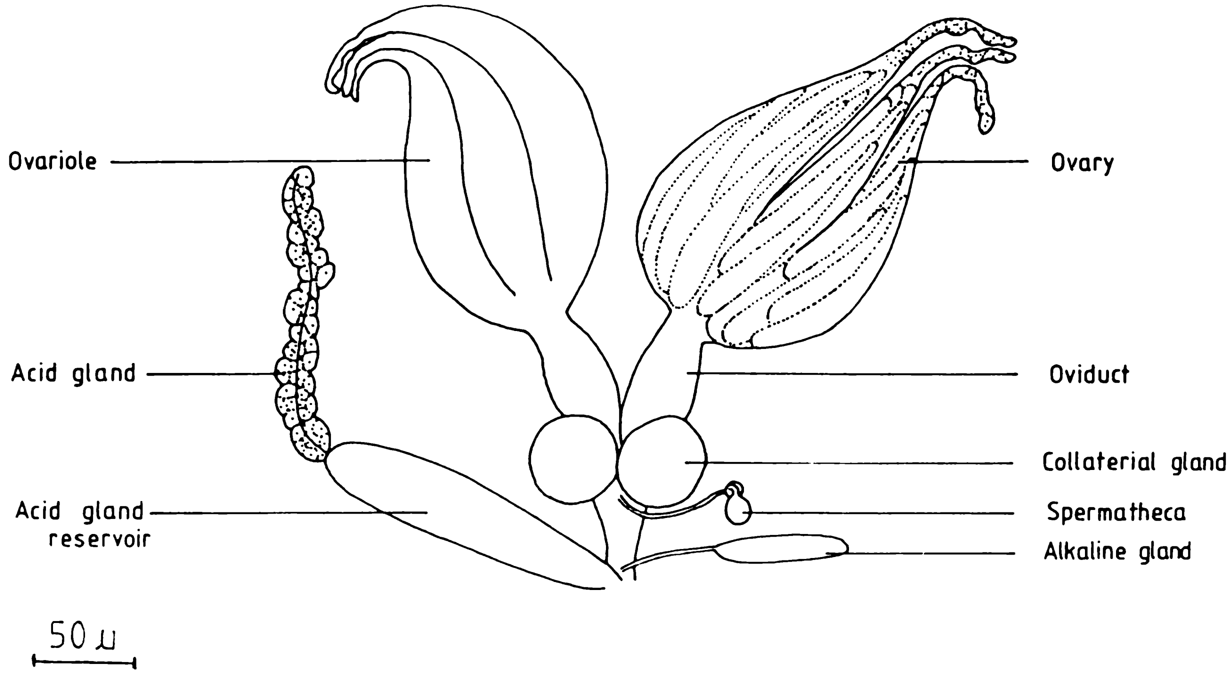


Fig 10:6 Internal reproductive system of the female *C. scolypopae*.

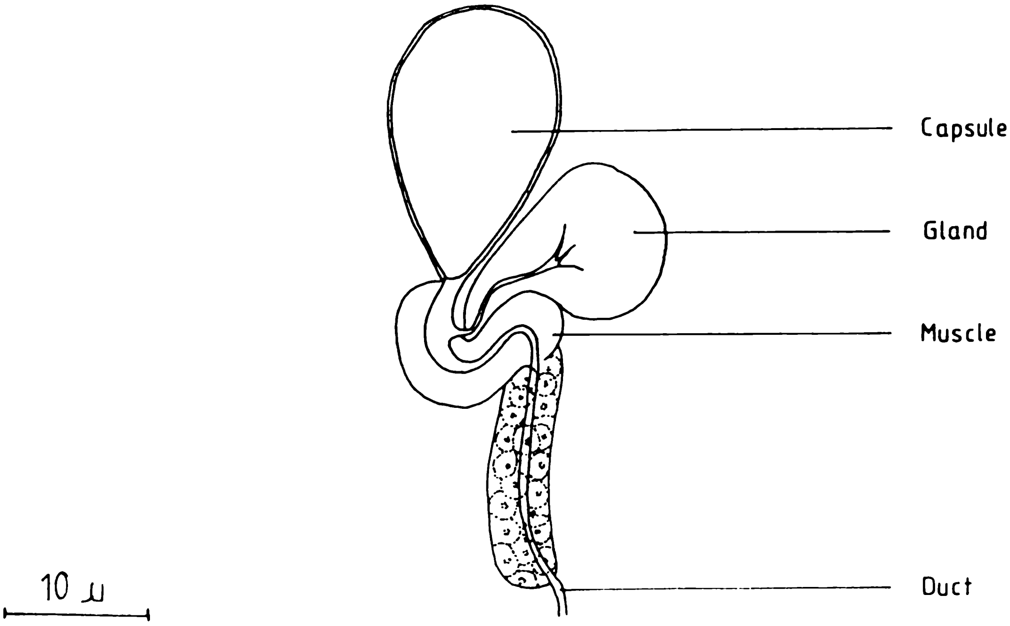


Fig 10:7 Spermatheca of *C. scolypopae*.

glandular part appears to be made up of loosely linked large cell masses with a fine central duct, instead of being a tubular gland. These cell masses are attached to the anterior end of a thin-walled reservoir. In general in Hymenoptera the secretion of this gland is described as venom. Possibly this secretion could cause the observed rapid breakdown in yolk structure of the host egg.

ii, External morphology

The ovipositor mechanism (Fig 10:8) at rest extends the full length of the abdomen and extrudes a short distance beyond. This is longer than in most Aphelinidae species were it usually extends from about one third of the way down the abdomen (Copland 1976). The increased length is an adaption to the depth of the embedded host eggs. The entire mechanism is similar to that of *Marietta picta* (Andre), described by Domenichini (1953). In common with other chalcids, it consists of 3 basic elements. Close to the thorax is a pair of semicircular sheets from which the stylets sheath and inner ovipositor plates bearing terminal palps project backwards. The outer ovipositor plates articulate with the fulcral plates, which pivot about the semicircular sheets, allowing the up and down motion of the stylet. The anterior third of the ovipositor mechanism is overlapped by the sternal sclerites which are very weakly sclerotised and form a transparent sheet, featureless apart from a few setae.

The semicircular sheets provide attachment for muscles at the dorso-posterior edge, where the plates extend back past the fulcral plates, and at a ligament in the middle of the crescent shaped posterior edge. The curved ramus edge of the sheet has a ridge that engages with a groove in the stylets. In *C. scolypopae*, the ramus

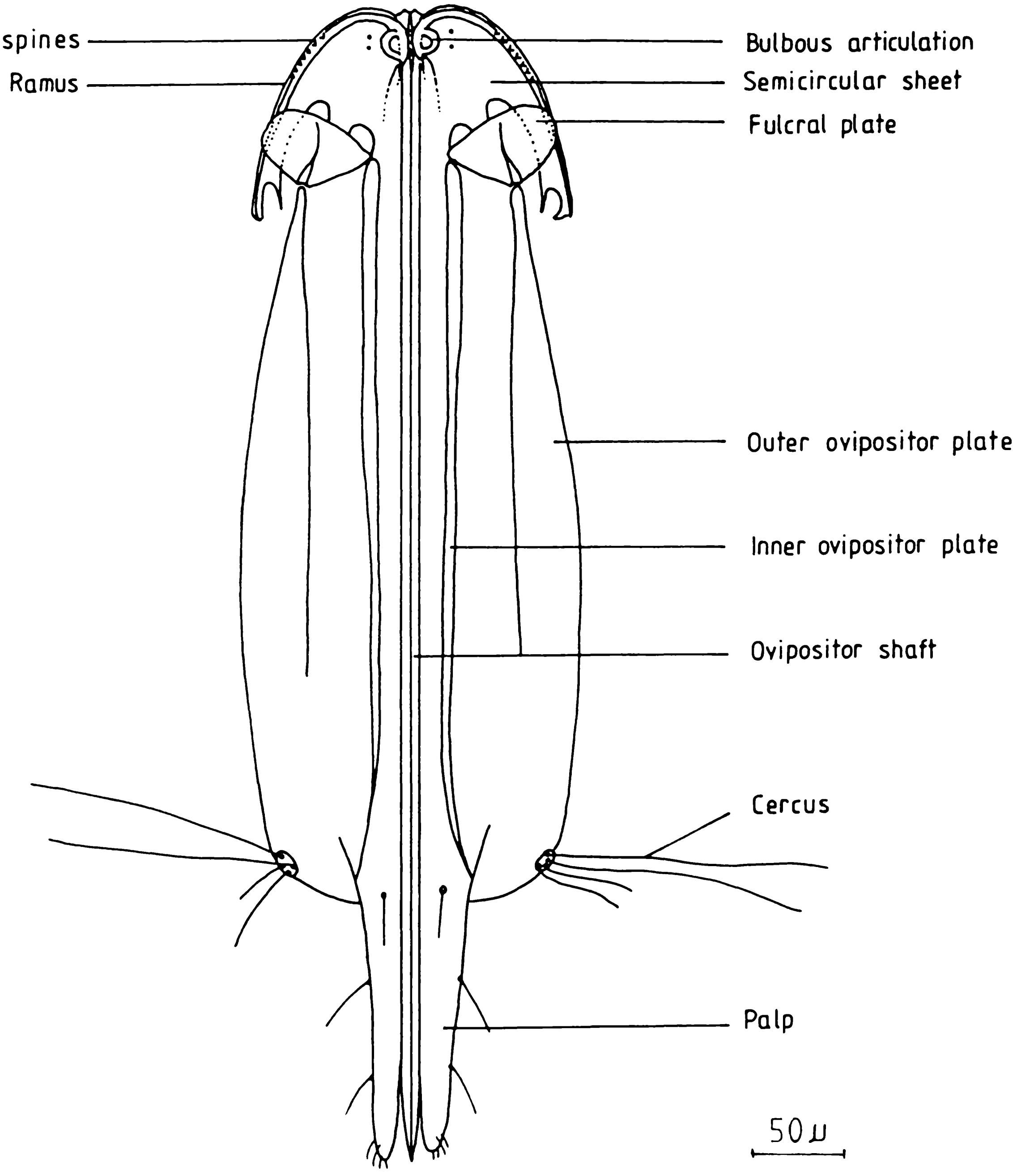


Fig 10:8 External female reproductive organs of *C. scolypopae*.

appears long compared to the aphelinid species studied by Copland (1976) and may be an adaption to the depth of the host eggs. There are 7 ramus spines which Copland (1976) thought may monitor stylet movement or the rotation of the ovipositor. He found 6 ramus spines in most species although more were associated with the long ovipositor of *Azotus atomon* (Walker). The stylet sheath is a continuation of the curved edge of the semicircular sheet. The two sheath elements form the ovipositor shaft down which the eggs can pass and is a strong and flexible drilling organ. At the distal end of the stylet sheath are a series of teeth. At the proximal end the sheath elements bear large bulbous sockets which articulate with projections on the semicircular sheets and to which a further muscle is attached.

The inner ovipositor plates lie to each side of the ovipositor shaft and are long continuations of the basal part of the sheets. A prominent ridge along most of their length provides attachment for muscle which unites them with the outer plates. At the base of this ridge the inner plates articulate with the fulcral plates. These are roughly triangular in shape with a thickened base near the articulation points and thining out at the apex.

According to Copland and King (1971), the stylets are projections from the apex of the fucral plates. They pass around the arms of the semicircular sheets between the bulbous articulations and form the ovipositor shaft with the stylet sheaths.

During oviposition, the ovipositor shaft rotates at the bulbous articulation to a position 90° from the rest of the abdomen. The transparent sheet, formed by the sternal sclerites, is stretched over the uppermost portion of the shaft and although does get pushed up a little at the end of drilling, appears to prevent the shaft being embedded the full length.

b, Male reproductive system

i, Internal morphology

The minute size of the male made dissection a near impossibility. The abdomen was pulled apart in a drop of Ringers solution and the findings are presented diagrammatically in Fig 10:9.

No references were found to the male internal reproductive organs of an aphelinid. Those of an eulophid *Dahlbominus fuscipennis* (Zett) (Wilkes 1965) and chalcid *Pteromalus liparae* (D'Rozario 1942) were somewhat different. Some spermatozoa were found in the long, tubular testes, but most were concentrated in the seminal vesicles. The only trace of the vas deferentia was a narrowing of the testes at their junction with the seminal vesicles. At the posterior end of each seminal vesicle is a cup-shaped organ which may correspond to the vesicular pocket in *D. fuscipennis* (Wilkes 1965). These empty into the ejaculatory canals which have very thick walls, possibly glandular or muscular in function. The accessory glands are possibly of ectodermal origin. They are round with a white granular appearance and have fine ducts that enter the ejaculatory canals before they unite to form the common ejaculatory duct. since most males mate soon after emergence, it was thought that in unmated males the testes may differ in shape from those already examined. However, dissection of males from host eggs prior to emergence showed identical morphology with no sign of spermatozoa in early stages of development. It is possible that sperm production is completed during the pupal stage, and owing to degeneration of the testes, spermatozoa are mainly found in the seminal vesicles ready for immediate mating at emergence.

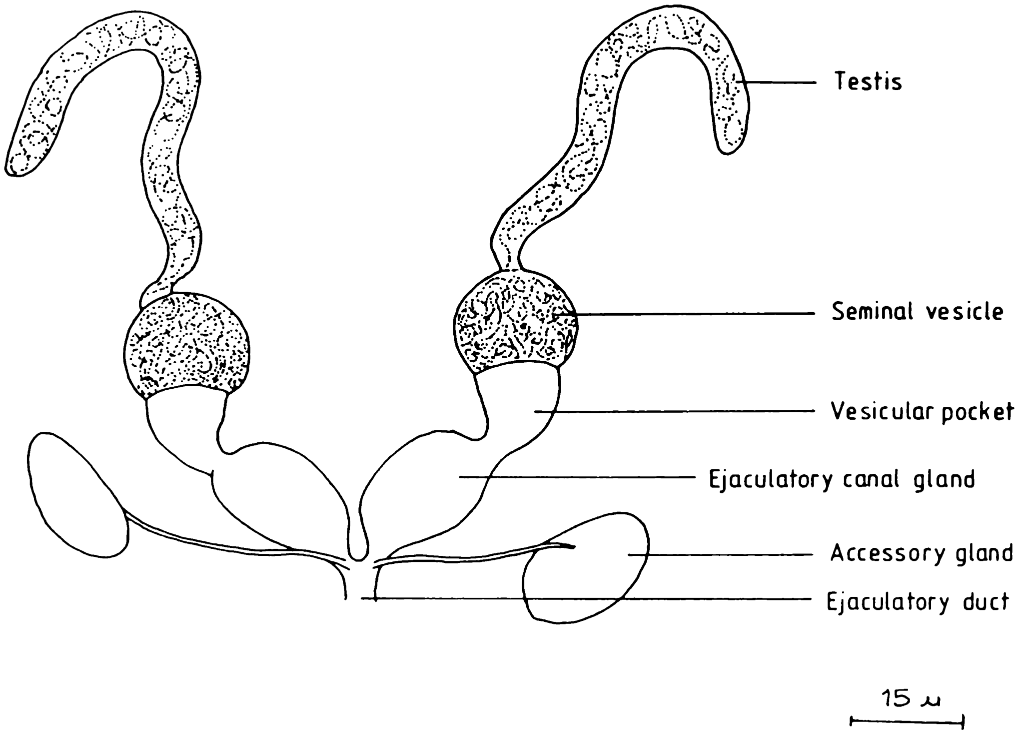


Fig 10:9 Male internal genitalia of *C. scolypopae*.

ii, External morphology

The male external genitalia are shown in Fig 10:10 and the naming adopted is that used by Snodgrass (1941) in his study of the male genitalia of Hymenoptera. The aedeagus, or penis, is a cylindrical tube which widens in the basal part before tapering at both ends. In the centre is the ductus ejaculatorius which opens at the extreme posterior end. *C. scolypopae* has a pair of fingerlike parameres, each with a single sensory hair at the terminal end. On the inside and parallel to the parameres are a pair of digiti or claspers, each ending with two strongly chitinised hooks. Each digitus is joined to the basiparamere with no distinct junction, unlike the Chalcidoidea species studied by Snodgrass (1941).

IV ADULT BEHAVIOUR

1, Mating behaviour

Most Hymenoptera mate immediately after emergence if the opposite sex is present (DeBach 1964) and this is the case with *C. scolypopae*. Most of the mating behaviour appears typical of the Aphelinidae cited by Gordh and Debach (1978). The male becomes excited within 1 cm of an unmated female and runs after her with wings vibrating occasionally. The male, with some difficulty, mounts the thorax of the moving female and vibrates her antennae with a rapid flicking action of his first pair of legs and tapping with his own antennae. The first response of the female is to stop moving. After half to two minutes the female's antennae droop to the ground, she rocks forward a little, the male slips back with his wings rotated past his head, turns the tip of his abdomen under that of the female and attempts to copulate before she

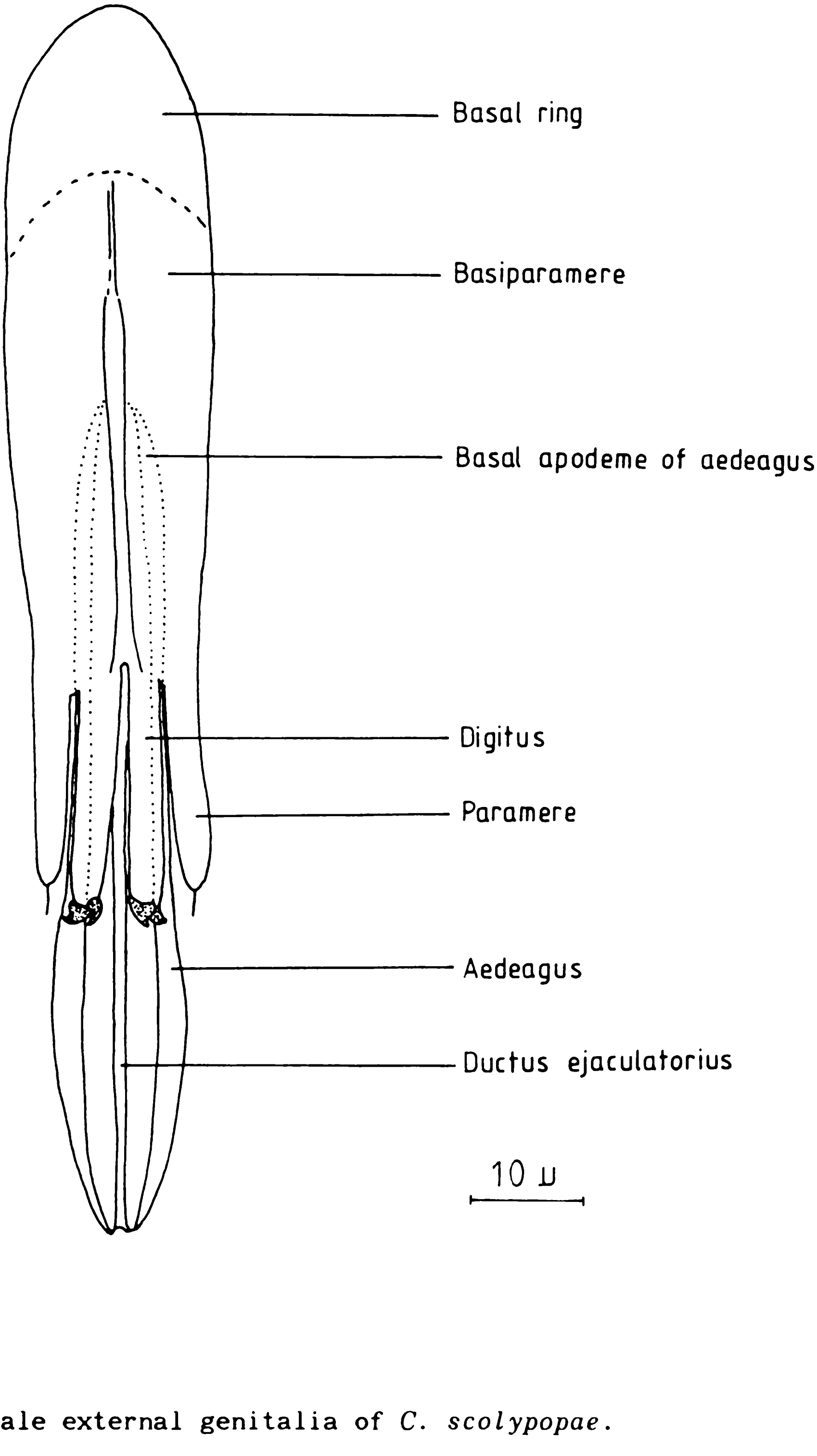


Fig 10:10 Male external genitalia of *C. scolypopae*.

moves again. The flicking, tapping and backwards motion of the male is often repeated several times before copulation is finally successful. The use of the forelegs differs from the usual male antennation in other aphelinidae where either the antennae are fanned on or near the female, or contact is made with the antennae on the female body. Gordh and DeBach (1978) suggested that fanning enabled males to perceive their own pheromone output and adjust the level to keep the female quiescent. However, it seemed from the behaviour of the female, that the rapid and vigorous flicking of her antennae by the male subdued the *C. scolypopae* female in a more physical manner, perhaps by causing a sensory overload. While in this state of disorientation, with her antennae hanging limply, she was unable to resist the male. After mating the female showed great resistance to any further attention by males.

2, Adult nutrition and longevity

To assess the longevity of *C. scolypopae* adults, newly emerged adults were held in test tubes at room temperature in indirect daylight, and fed either with a smear of honey or *Scolypopa* honeydew or starved. Most starved adults died within 24 hours, those fed with honey live an average of 15•5±1•7 days (n=37) with a maximum of 56 days while the lifespan of those fed on honeydew was 5•3±0•5 (n=57). Honeydew was very susceptible to moulds which may have influenced these results. It was noticable that *C. scolypopae* adults became increasingly more active as light intensity increased and in bright light, even when fed with honey, longevity was reduced to 2-3 days. Water was provided in a few cases by filling fine glass tubing with a little saturated cotton wool but mortality increased as adults became trapped in the honey which became fluid in the presence of water.

During the time of *C. scolypopae* adult activity at the Steele's Farm site there were almost no nectar sources available as blackberry had ceased to flower. Even though not observed in the field, it is probable that *Scolypopa* honeydew is the main food source for *C. scolypopae* adults. Host honeydew forms part of the diet of *Encarsia formosa* (Gahan) (Hymenoptera:Aphelinidae) females who live for 15-30 days (Agekian 1981). Host feeding is common in many species of Aphelinidae such as *Aphytis* (Gulmahamad and DeBach 1978, Alexandrakis and Neuenschwander 1980) and *Aphelinus* (Hamilton 1973) and may kill as many hosts as parasitism itself. However the depth of the buried host egg prevents *C. scolypopae* using it as a protein source.

3, Oviposition behaviour

At the study site the *C. scolypopae* adults emerge in close proximity to the new generation of host eggs. The parasite adults do not fly readily and often land only a few centimetres away if disturbed, preferring to move by running. Adults show strong phototaxis and negative geotaxis so presumably after emergence move upwards through the plant layers from the denser older material to the more open material where the current generation of *Scolypopa* is ovipositing. Females search by running along woody plant material with the flagella of the antennae held vertically, tapping the surface. Sight apparently plays only a small role as females turn towards *Scolypopa* oviposition tufts only if passing within 1 mm.

Once found, the female investigates the *Scolypopa* oviposition scar with her antennae. This is done with the flagella of the antennae held vertically and moved rapidly up and down. This process has been termed drumming (Edwards 1954). The female selects one oviposition tuft and after drumming in the immediate vicinity, stops, turns, flexes her body and taps with the tip of her abdomen. This tapping apparently places the ovipositor tip in position for drilling. The drumming and tapping may be repeated several times before drilling commences. The time taken by females from first finding an oviposition scar till drilling has commenced is usually about 10 minutes. The body is then straightened and the full length of the ovipositor is visible at a 90° angle to its resting position. The female starts to drill through the plant tissue adjacent to the frass left by the *Scolypopa* female. Almost the full length of the ovipositor is inserted through the plant tissue to the host egg. Once eggs are laid, the ovipositor is withdrawn and cleaned with the hind legs before the next egg is investigated. The time taken for drilling and oviposition varies from 6-38 minutes.

C. scolypopae appears specific to *S. australis* in New Zealand. Eggs of *Sephena cinerea* (Homoptera:Flattidae) are superficially similar to those of *S. australis* and were laid amongst them in bracken and blackberry in the study area. However, although females would attempt to oviposit in them in the laboratory, no parasites were reared from them and no parasitism was detected in samples from the study area. A high percentage of *S. cinerea* eggs were found parasitised by an unidentified *Centrodora* species at Ruakawa Falls, 41 km. north of Wanganui, but the *S. australis* eggs there were untouched. The larvae of the unidentified species were yellow and larger than *C. scolypopae* but otherwise were identical morphologically. The few adults reared were a little larger than *C. scolypopae* and were a golden yellow colour.

CHAPTER ELEVEN

INFLUENCE OF HOST PLANT ON PARASITISM

I INTRODUCTION

Parasitism of *S. australis* eggs laid in bracken was much greater than that found in eggs laid in blackberry, as was shown in Chapter 6, (Fig 6:1). The wide divergence between levels of parasitism in blackberry and bracken indicates that host plant factors play an important role in the oviposition behaviour of *C. scolypopae* females.

Plants can influence parasitism in several different ways. Olfactory responses to the host plant are common and parasites may show preferences between species. For instance, *Itoplectis conquisitor* (Hymenoptera:Ichneumonidae) is attracted to the odour of Scots pine (*Pinus sylvestis*) more than that of the Red pine (*P. resinosa*) and thus gives correspondingly higher levels of parasitism on the former (Arthur 1962). *Apanteles flaviceps* (Hymenoptera:Braconidae) prefers frass from stem borers in sorghum and corn to that of sugarcane (Inayatullah 1983). Parasitism may be influenced by physical attributes of the plant such as surface texture in the case of *Trichogramma* (Flanders 1937). Hosts in or on differing parts of the same plant may vary in vulnerability. Females of *I. conquisitor* are unable to parasitise pupae in buds protected by needles and parasitism was higher in small than in large buds (Arthur 1962). Carnegie (1980) considered the growth habits of host plants to be a factor causing the low levels of parasitism by *Ootetrastichus beatus* (Hymenoptera:Eulophidae) and *Oligosita numiciae* (Hymenoptera:Trichogrammatidae) in sugarcane compared to other host plants. The minute and delicate egg parasites were considered to be able to find host eggs more easily in the low-lying and dense indigenous grass than among the more widely separated leaves of a field of sugarcane.

II OBSERVATIONS

S. australis has an extremely wide range of host plants and in most cases *C. scolypopae* emerge in the vicinity of the host eggs. Therefore it seems unlikely that a specific plant odour would play a role in the attraction of the parasites. However, odours could be important in the detection and acceptance of a host egg. Females closely investigate potential host oviposition scars with their antennae and the odour of fresh wood tufts may well influence acceptance or rejection.

Blackberry and bracken differ in structure. Dead blackberry stems are round in circumference, have a large soft central pith and are surrounded by a woody layer consisting of vascular tissue and an outer bark layer. The surface is relatively rough and scattered with thorns. Dead bracken stems have no central pith and are hard throughout. The surface is smooth with longitudinal ridges and planes. *S. australis* females generally oviposit on the ridges. In Chapter 5 and Appendix 1 it was shown that females lay more and larger egg batches on blackberry than bracken, probably because of the ease of ovipositing in the soft pith. It also seemed likely that the pith enabled eggs to be laid at greater depths in blackberry than occurred in bracken. If true, blackberry would have a degree of immunity in that it would make oviposition by *C. scolypopae* females more difficult.

It was decided to test the hypothesis that egg depth varied with plant species and in turn influenced parasitism levels. Blackberry, bracken, barberry and black bindweed stems bearing oviposition scars were collected from a single 2 m^2 plot in block BT in May 1983 and 1984. In the laboratory, each egg scar was opened longitudinally with a scalpel to expose the intact eggs in situ. The minimum distance between the stem surface and the egg was measured with the aid of an eyepiece graticule in a binocular microscope. These measurements had to be done before the end of May as embryo or larval development caused the egg to swell soon after.

To ascertain the maximum depth *C. scolypopae* females could oviposit successfully, the lengths of ovipositor from just below the bulbous articulation to the tip were measured on females emerging from laboratory maintained host eggs. Also the time taken for females to oviposit in blackberry and bracken was recorded to see if this varied. Time was recorded from the commencement of drilling to the withdrawal of the ovipositor.

The average length of the ovipositor was 0•60+•01 mm and ranged from 0•48 to 0•65 mm (n=21). This does not mean a female can oviposit in eggs 0•65 mm deep. The ovipositor must pierce the egg and also a portion of the ovipositor shaft remains above the surface even when it is embedded in the wood to the maximum limit. These two factors would combine to make the maximum depth of egg that an average female could successfully parasitise to be more like 0•5mm.

Females took slightly longer ovipositing in bracken averaging 18 min 14 sec (s.e. 154 sec n=22) compared with 13 min 2 sec (s.e. 137 sec n=17) on blackberry. This difference is most likely caused by bracken wood being harder, suggesting that difficulty in drilling was not a factor contributing to the lower levels of parasitism in blackberry. Alternatively, since no inspection was made to see if females had actually laid eggs, it is possible that some females, on blackberry in particular, may have withdrawn early after reaching maximum depth without having penetrated the host egg.

The egg depth results are presented in Fig 11:1. It can be seen that the distribution of host eggs in blackberry is deeper than on blackberry and bindweed. When compared with the average length of *C. scolypopae* ovipositors and the probable maximum depth of penetration of 0•5mm associated with it, it is apparent that egg depth plays an important role in regulating levels of parasitism. Many host eggs in blackberry are beyond reach and this directly results in less parasitism especially if eggs are laid deeper than 0•4 mm. In barberry, there are two peaks of egg density. That shallower than 0•3 mm, with correspondingly high parasitism, consists of eggs laid in the hard, narrow thorns whereas the other peak, mainly above 0•4 mm, with lower parasitism, is mainly eggs laid in the softer stems. Thus within a single plant, susceptibility to parasitism varies with the plant part, depending on the depth of the eggs.

Egg depth beyond that of the average parasite's capability would not only cause failure to penetrate the egg. It would increase the likelihood of the female leaving the area and also the possiblity of her failing to deposit her full egg complement before death if she remained. This would confer a degree of immunity and reduce the rate of parasitism in the plant as a whole. When the percentage parasitism for each host plant is plotted against mean egg depth for the plant (from Fig 11:1), a linear relationship is found($t=4{\cdot}243$, $P\approx0{\cdot}05$) (Fig 11:2). That the line infers greater than 100% parasitism at shallow depths is reasonable as superparasitism occurs often. Although only 4 species in the area were assessed, the results support the hypothesis that the differing levels of parasitism is caused by the depth of host

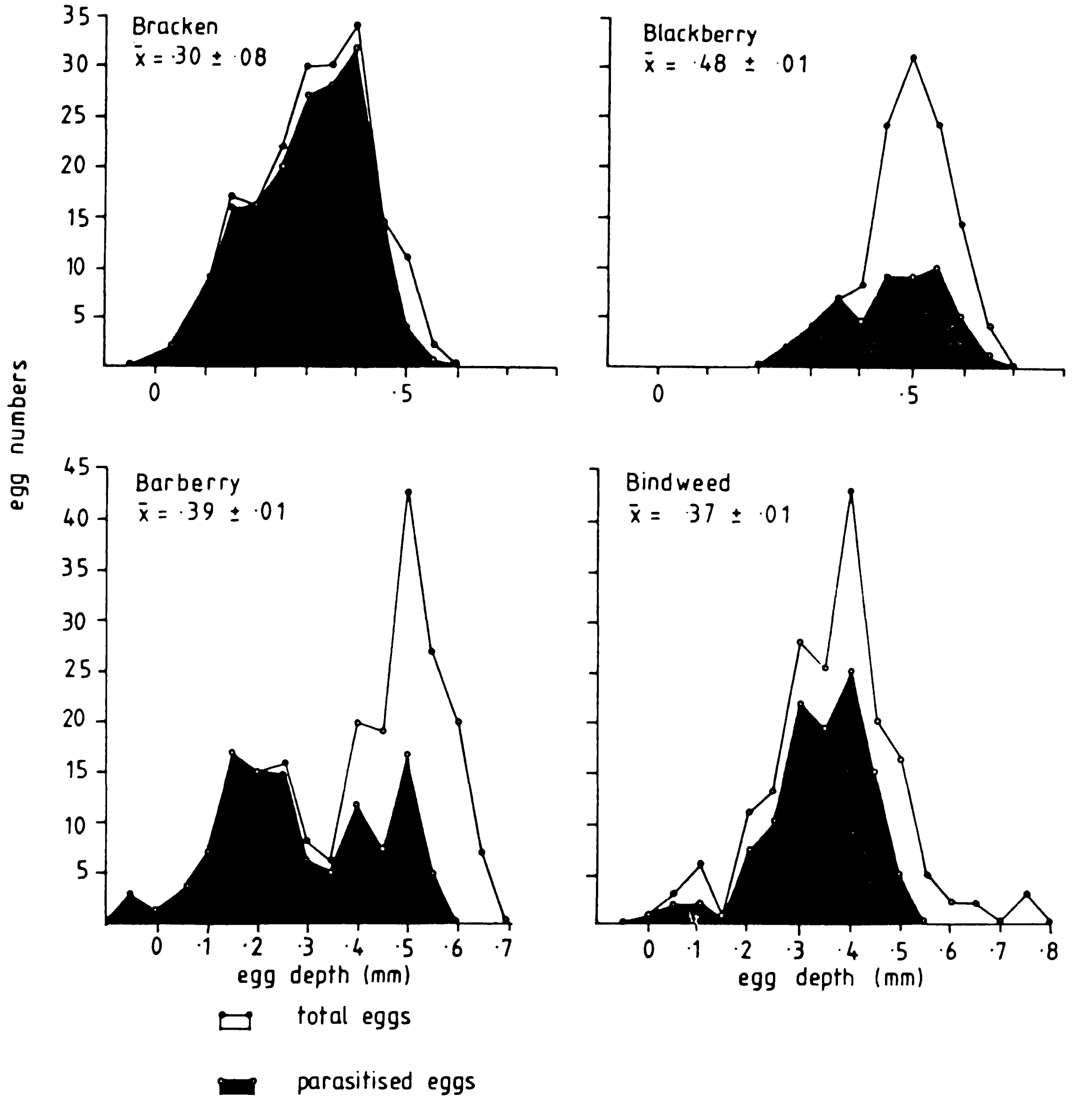


Fig 11.1 Depth below surface of total and parasitised *S. australis* eggs in four plant species, Block BT, May 1983 and 1984. (x̄= mean depth±s.e.).

eggs in that plant. This was reinforced when egg batches were collected from tutu (*Coriaria arborea*) and tree fern (*Cyathea* sp.) at Karapiro. Even though from another site where the overall level of parasitism may differ, these plant species had the same relationship between percentage parasitism and egg depth (Fig 11:2). Eggs in tree fern were shallow and were heavily parasitised. Those in the flower racemes of tutu had high parasitism but the more abundant eggs in the stems were deeper and had lower levels. (Fig 11:3)

This interaction of egg depth and level of parasitism limits the effectiveness of *Centrodora scolypopae* and is possibly the main reason why *C. scolypopae* cannot reduce *Scolypopa australis* to levels below pest status in the Northern North Island. In any bush or waste area, a proportion of the population would be resistant to attack. Of particular note is resistance of eggs on tutu. It is the high populations of *S. australis* on tutu in summer that are responsible for honey poisoning in the Coromandel and Bay of Plenty areas.

As biological control is the only feasible method of controlling *S. australis*. these results provide important information that is relevant in any search for an exotic natural enemy. The deeply laid eggs can be regarded as an empty niche and if a hymenopteran parasite is considered, it must be one with an ovipositor longer than that of *C. scolypopae*. An alternative could be to manipulate the present parasite. Females resulting from a solitary larva per host egg are larger with longer ovipositors. A small change in the sex ratio would increase the proportion of females able to parasitise the deeper eggs. The planting of tree ferns or other 'hard' plants or the elimination of 'soft' species in areas from which *S. australis* spills over into horticultural crops could enhance the parasite populations and the damage caused by *S. australis*.

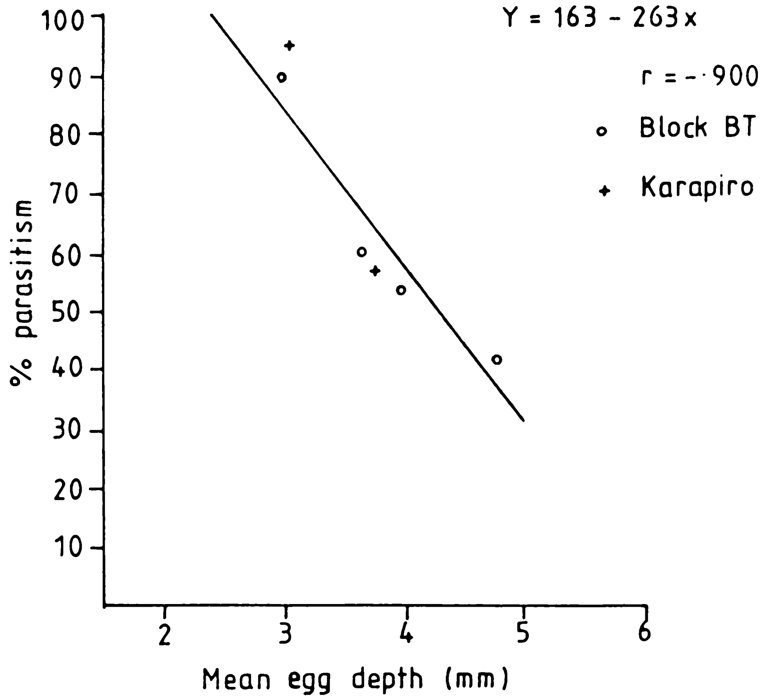


Fig 11:2 Relationship between percentage parasitism and mean egg depth in plant species at Rukuhia (Block BT) and Karapiro.

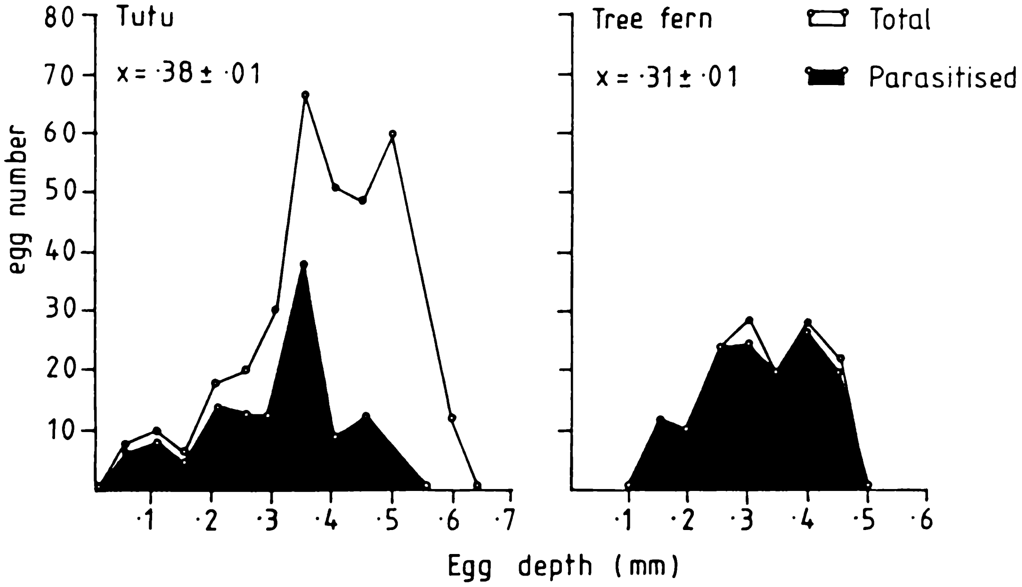


Fig 11:3 Depth of total and parasitised *S. australis* eggs in Tutu and Tree fern, Karapiro, May 1984.

CHAPTER TWELVE

SEX RATIO AND SUPERPARASITISM

I INTRODUCTION

During examination of *Scolypopa* eggs for causes of mortality, multiple parasite oviposition scars were frequently observed. However, the number of *C. scolypopae* larvae in these host eggs did not appear greater than normal. Thus it was uncertain whether parasite females did oviposit or were able to distinguish previously parasitised eggs with their ovipositors after insertion in the host egg. Therefore a study was undertaken to assess parasitised eggs for possible evidence of superparasitism or discrimination and how these factors affected the numbers of parasite larvae reaching maturity in each host egg.

Cumber (1966) noted that *S. australis* eggs may nourish one to four individuals, but usually two are present, one of each sex. He found the overall sex ratio of emerging adults approaches 2:1 in favour of the females. Male and female third instar larvae are easily distinguished by size at maturity. As larval numbers were to be assessed, it was decided to record the number of each sex and thus obtain an estimate of the sex ratio within the trial area.

II METHOD

During August 1983, *S. australis* egg batches laid in bracken were collected along the length of each block in the trail area. Eggs were extracted from the twigs by twisting the wood so that it split along the oviposition scar and the eggs fell into a petri dish below. The host egg chorion was then cleared with 70% ethanol so that parasite larvae could be counted and sexed. *C. scolypopae* leave a small raised protruberance at the site at which the ovipositor was inserted in the host egg, possibly a small amount of host yolk which has exuded out and coagulated. This is transparent initially but becomes amber within a few days of oviposition. With the use of a low power stereomicroscope these protruberances can be counted on the dorsal surfaces of the host eggs. Because of the relatively large egg surface area and small size of the oviposition scar, the chance of two females ovipositing at exactly the same site was small and in this study such eggs were found to be extremely rare. For each egg viewed the number of parasite oviposition scars, parasite progeny and stage of development was recorded.

The process was repeated during March 1984, when *Scolypopa* eggs in blackberry were also sampled, and again in June 1984.

III RESULTS

The pooled results from all blocks sampled at the three sampling times are presented in Tables 12:1-4. There were small but insignificant differences between blocks in the proportion of eggs with multiple oviposition scars at each of the 3 sampling times.

Table 12:2 shows that early in the season, superparasitism, as evidenced by the additional parasite oviposition scars, results in a greater number of parasite larvae in each host egg compared with that from a single oviposition. All stages of parasite development were found from eggs to fully mature lavae. Because of the rapid larval development, progeny from successive ovipositions within a single egg could be distinguished easily by size and development in most cases

Table 12:1 Numbers of oviposition scars and parasites in *S. australis* eggs parasitised by *C. scolypopae* in bracken, August 1983.

		oviposition scars			
		1	2	3	4
parasites/egg	1	44	21	8	1
	2	88	57	17	6
	3	0	6	3	0
	4	0	2	1	0
	N	132	86	29	7
mean parasites (±SE)/egg		1·65±·04	1·87±·07	1·90±·13	1·86±·14

Table 12:2 Numbers of oviposition scars and parasites in *S. australis* eggs parasitised by *C. scolypopae* in bracken, March 1984.

		oviposition scars				
		1	2	3	4	5
parasites /egg	1	92	7	0	1	1
	2	131	34	4	0	0
	3	3	45	2	1	0
	4	0	23	6	1	0
	5	0	0	7	0	0
	6	0	1	6	0	0
	N	226	110	25	3	1
mean parasites (±SE)/egg		1·61±·03	2·80±·07	4·36±·28	2·67±·88	1
mean larvae/oviposition		1·61±·03	1·40±·04	1·45±·09	0·67±·22	0·2

Table 12:3 Numbers of oviposition scars and parasites in *S. australis* eggs parasitised by *C. scolypopae* in bracken, June 1984.

		oviposition scars			
		1	2	3	4
Larvae/egg	1	84	27	14	4
	2	128	62	14	2
	3	0	6	0	0
	4	0	5	2	0
	5	0	0	0	0
	6	0	0	1	0
	N	212	100	31	6
mean parasites (±SE)/egg		1•60±•03	1•89±•07	1•81±•20	1•33±•21

Table 12:4 Numbers of oviposition scars and parasites in *S. australis* eggs parasitised by *C. scolypopae* in blackberry, March 1984.

	oviposition scars			
	0	1	2	3
N	152	84	19	3
mean parasites (±SE)/egg	0	1•79±•05	3•07±•22	2•3±•3

(see Plates 12:1-2). This provided visible evidence that superparasitism was occuring. It was apparent that the progeny from the first oviposition was dominant over the later individuals. Eggs laid into host eggs already containing third instar larvae failed to hatch; their contents became transparent and the chorion fragile. Eggs laid with earlier instars hatched, but the larvae failed to grow well, gradually assumed a dwarfed, dense white appearance and eventually disintegrated. Only when all individuals were about the same age did they all appear healthy at the time of the March 1984 sampling.

Comparison of the means of parasite oviposition scars (Table 12:2) shows that there were fewer larvae/oviposition found in eggs with multiple oviposition scars than in those with a single oviposition scar. It was also found in the March sampling that eggs containing third instar larvae were more likely to have multiple scars (x=1•78+•03) than the population as a whole (1•48+•03) (t=5•29, P<•001).

Tables 12:1 and 12:3, show that later in the season in July and August there is still a significantly greater number of parasite larvae in eggs with 2 oviposition scars than in those with 1 (1983 t=2•72 P<•01, 1984 t=3•59 P<•001), but the mean number of larvae per egg in the eggs with multiple oviposition scars is considerably lower than in March (Table 12:2) However, in the majority of host eggs containing 3 or more individuals, the parasites were small third instar larvae. They had unusual large clear globules in their gut which also had a curdled appearance. Healthy individuals at this time completely filled the host egg but these larvae barely filled half the available volume. Although still alive and thus included in the results, it is very doubtful that these larvae would mature. The occasional exceptions

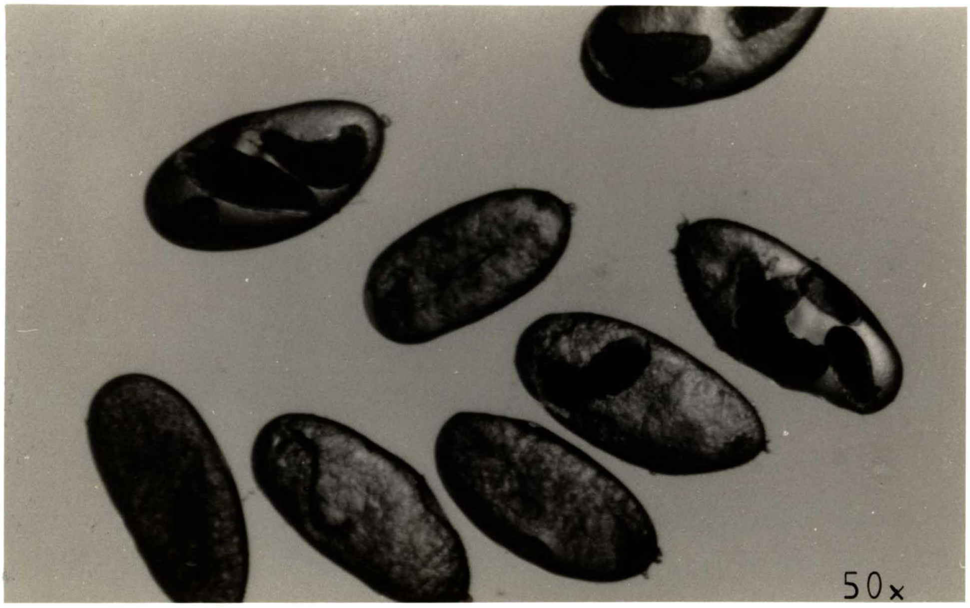


Plate 12:1 Sample of *S. australis* eggs showing occurrence of superparasitism.

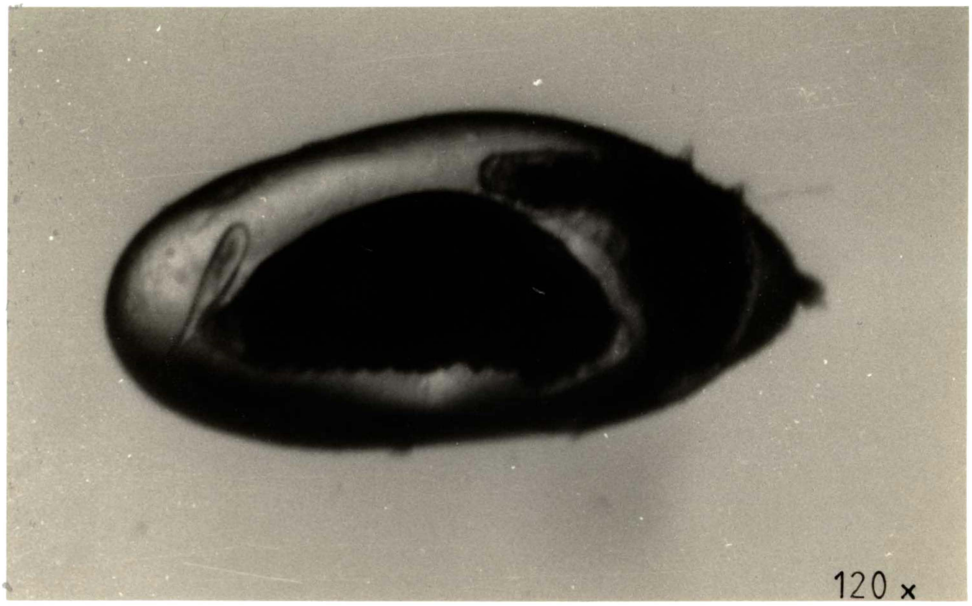


Plate 12:2 *S. australis* egg containing *C. scolypopae* egg and larvae from two seperate parasite ovipositions.

were eggs containing a female and two male larvae which had been laid by a single female.

Van Lenteren et al. (1978) tested for the occurrence of host discrimination by comparing observed parasite egg distribution with that of a Poisson distribution. If significantly different, the parasite was said to be able to distinguish parasitized from unparasitised hosts, even if superparasitism did occur. The distribution of oviposition scars within the host egg population for the combined 1984 samplings on bracken are presented in Fig 12:1 along with a Poisson distribution calculated with the mean number of oviposition scars/host egg as an estimate for λ.

In all three tables, the number of larvae resulting from only 1 oviposition scar/host egg is an estimate of the sex ratio of *C. scolypopae* juveniles. When a single egg is laid by a mated female, the resulting larva is always female as observed at pupation. It was soon apparent while sexing the larvae within the host eggs that when two eggs are laid, there is always one male and one female. In the rare occasions when more than 2 are laid, there is still only one female amongst the progeny. Table 12:3 shows that in June 1984 there were 212 host eggs with a single oviposition hole, 84 containing single larvae and the rest 2 larvae. Therefore there were 212 females and 128 males, giving a female:male ratio of 1:0•6. This ratio can be read directly from the mean number of larvae/host egg estimate of 1•60 where the residue above 1 is the ratio of males in the population. Thus Table 12:1 shows a female:male ratio of 1:0•65, and Table 12:4 shows that in blackberry, the ratio was 1:0•79. There were small but insignificant differences in the sex ratio between blocks in the three sampling times. There was a significant difference between blackberry and bracken in March 1984 ($P<\cdot05$).

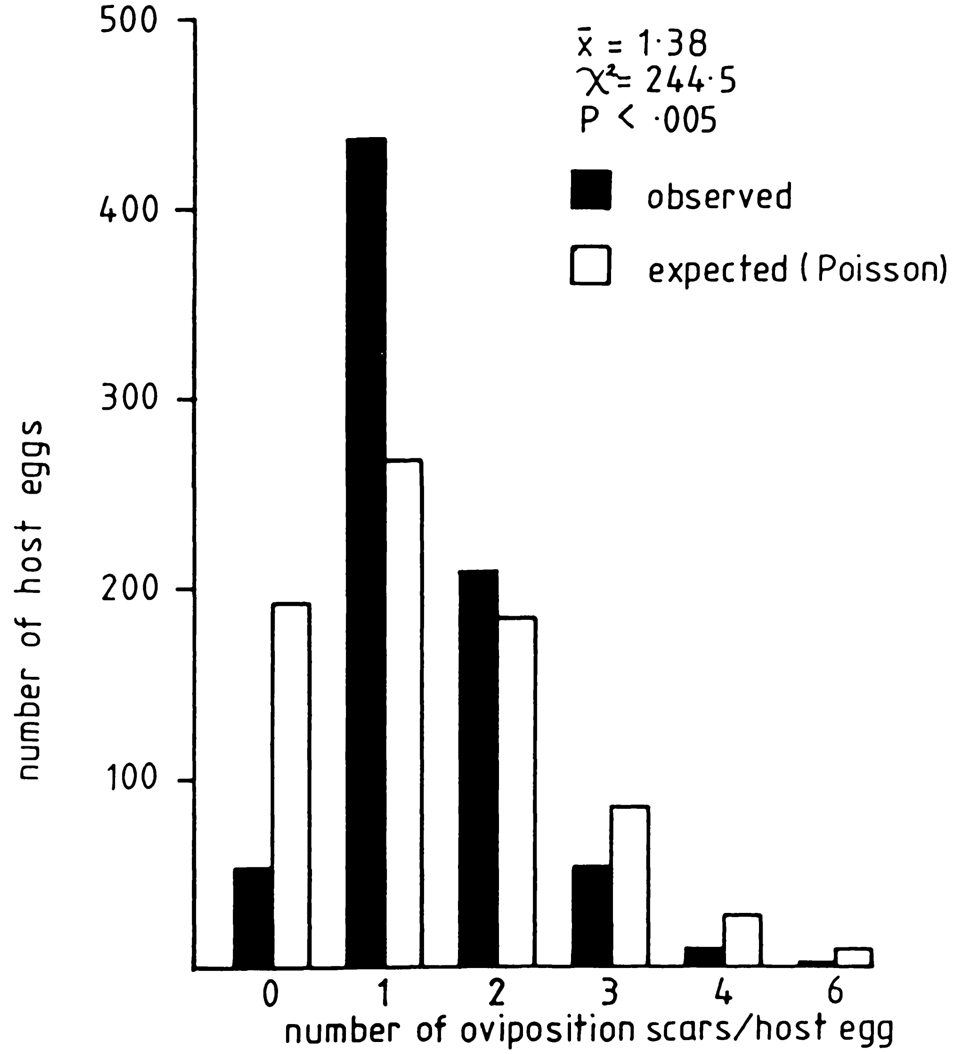


Fig 12:1 Comparison of observed parasite oviposition scar distribution and distribution expected if oviposition occurred at random (Poisson distribution).

In Fig 12:2 the proportion of superparasitised eggs in each block for both March and June samplings is plotted against the corresponding sex ratio (Mean larvae/egg for eggs with single oviposition scars), using the 1984 bracken samples. It is clear that number of males in the population increases as the level of superparasitism increases.

IV DISCUSSION

The examination of parasitised eggs during March 1984 gave clear evidence that superparasitism occurs in *Centrodora scolypopae* populations. Even though there appeared to be significantly fewer eggs per oviposition in superparasitised eggs (Table 12:2), it is probable that superparasitising females do not reduce the number of eggs deposited significantly. Host eggs containing larger larvae were more likely to be superparasitised than the rest of the population. These larger larvae, in many cases, had completely eliminated all traces of the later parasite eggs by sampling time, thus giving an underestimate for actual parasites laid in each host egg. This is most apparent in the results for the 4 and 5 oviposition holes per egg in Table 12:2.

It is apparent that the progeny from the first oviposition was dominant and eliminated the younger individuals by physiological suppression. A variety of possible mechanisms for such supression have been suggested. Early writers proposed a 'toxic secretion' (Timberlake 1910, Muesebeck 1918). The term 'cytolytic enzyme' was used by Spencer (1926), Thompson and Parker (1930) and Johnson (1959). Tremblay (1966) hypothesised that older larvae withdraw nutrients from the host haemolymph that are essential to the development of the younger larvae. Fisher (1971) suggested that the respiratory requirements of the

```
             1.70+
                 -
                 -
                 -                                       *
                 -
             1.65+                                      *
  Mean           -
larvae/egg       -
(sex ratio)      -                                         *
                 -
             1.60+
                 -                                 *
                 -
                 - *
                 -
             1.55+                    *
                  +---------+---------+---------+---------+---------+
                  25        30        35        40        45        50
                                 Percent superparasitism
```

Fig 12:2 Relationship between sex ratio of *C. Scolypopae* and percentage superparasitism in 1984, using individual block values.

younger parasites are not satisfied in hosts already containing older larvae so that the younger ones died of oxygen lack. A combination of mechanisms is likely. Certainly almost all traces of competitive younger larvae are eliminated by July and August. A specific toxin may also be produced to suppress competition. The production of 3 healthy larvae from the occasional single 3 egg oviposition and unhealthy larvae from multiple ovipositions on or about the same day indicates that some sort of chemical suppression exists. From Table 12:1 it can be seen that about 48% of the parasitised eggs in bracken had been superparasitised. The following year, between 38-39% of parasitised eggs were superparasitised . The level in blackberry was lower (21%) presumably reflecting the lower level of parasitism in blackberry overall. Superparasitism thus resulted in the wastage of approximately 65% of the parasite eggs laid in bracken in 1983 and 47-52% in bracken and 24% in blackberry in 1984. This was the largest mortality factor in the parasite population in these two years.

Initially it appears that *C. scolypopae* females show little discrimination in oviposition. However Fig 12:1 shows that when oviposition scar distribution is compared with the distribution that would have been obtained had the females oviposited at random (Poisson distribution) the two are significantly different. Most notable is the higher than expected number of single ovipositions indicating that *C. scolypopae* females can discriminate between parasitised and nonparasitised host eggs. Observations of female behaviour show that females usually take about 10 minutes examining the vicinity of a prospective host egg with their antennae before commencing tapping and drilling. The ovipositor probably plays no role in discrimination as it appears from Table 12:2 that once it is inserted, eggs are almost always laid. The high level of superparasitism found may result from several factors. Firstly, in both 1983 and 1984, the population of *C. scolypopae* was high compared to the number of host eggs available (Chapter 6). On some bracken fronds, parasitism reached 100%. A searching female may have an increasing urge to oviposit and when only finding parasitised hosts, resorts to superparasitism. Salt (1934) recognised this phenonomen and attributed it to a failure of restraint. Secondly the *C. scolypopae* oviposition period is over 6 weeks long. If discrimination between parasitised and nonparasitised eggs results from an odour or 'spore effect' as suggested by Flanders (1950), then rain and general weathering could diminish its effectiveness. Thirdly, the host egg is laid deep in wood. There is a relatively large external surface area above to search and through which drilling can occur. A female could miss another's 'marker' on this rough surface.

From the oviposition results it can be seen that *C. scolypopae* females lay 1, more frequently 2 and rarely 3 eggs per host egg. There is always a single female in each egg and any additional larvae are male. Most Hymenopteran females possess a spermatheca in which spermatozoa are stored after mating. According to Flanders (1937) the spermatheca has also a sex determining function. As the egg passes down the oviduct, the spermatheca discharges spermatozoa if the proper stimulus is present. The diploid egg develops into a female. If unfertilised, a haploid male is produced.

Like most parasitic hymenopteran species, *Centrodora scolypopae* exhibits this facultative parthenogenesis or 'arrhenotoky'. Some have obligatory parthenogenesis which is termed 'thelyotoky'. An aphelinid example of a thelyotokous species in which a male is virtually unknown is *Aphytis chilensis* Howard (Rosen and Eliraz 1978), a genus closely related to *Centrodora*. Deuterotoky is a term used for species which are normally thelyotokous but occasionally males are produced.

Encarsia lutea Masi rarely produces males when reared from whiteflies *Trialeurodes abutilonea* and *T. vaporariorum* but if lepidopterous eggs are parasitised only males will result (Stoner and Butler 1965).

From Tables 2:1-3 it can be seen that the sex ratio for *C. scolypopae* in host eggs laid in bracken was 1:0•6 (1•7:1) in favour of the females. This appears to be flexible however and varies with plant species as indicated by the higher male ratio in blackberry. Cumber (1966) listed numbers of males and females emerging from many plant species. When all samples of less than 50 individuals are excluded, his results indicate that the female:male ratio may vary from 1:1 in *Pteridium* to 4:1 in *Coriaria*.

Fig 12:2 shows an increase in the number of males with increasing superparasitism. This may be the response of females to the increasing levels of parasitism. Females searching unsuccessfully may have an increasing urge to oviposit and once finding a suitable host, lay more than one egg. It has been observed in the laboratory that host-deprived day old females may lay up to 8 eggs in their first oviposition when presented with suitable host eggs.

CHAPTER THIRTEEN

SYNCHRONISATION OF HOST AND PARASITE

The success of a parasite depends on the synchronisation of its life cycle with that of the host. *C. scolypopae* overwinters in an early phase of the prepupal stage in an apparent state of diapause and does not pupate until host adults appear in mid summer. *S. australis* is univoltine, overwintering in the egg stage. It has no diapause but a very long period of continuous development (Fletcher and Anderson 1980). The relationship found between population nymphal development and cumulative day degrees, demonstrated in Fig 7:7 indicates that temperature, and *S. australis* development and population growth are closely linked.

Insect phenology is concerned with the timing of recurring biological events in relation to key environmental factors and is fundamental to understanding population growth, species distribution and species interactions (Tauber and Tauber 1976). In order to elucidate field observations of both host and parasite development and to aid in the understanding of how *C. scolypopae* manages to synchronise adult emergence with the oviposition period of the host, experiments on the response of both host and parasite to temperature were conducted over the period of this study. Because of the univoltine life cycle of the host, experiments were of long duration and unfortunately prone to failure from disease and desiccation. As well, it was only too easy to miss checking for stage of development of a sample in which nothing visible had occurred for several months.

Experiments concerned with the phenology of the host are presented and discussed first, followed by those on the parasite.

I INVESTIGATIONS ON DEVELOPMENT OF S. AUSTRALIS

1, Duration of the egg stage in outdoor conditions.

To ascertain the duration of the egg stage under near natural conditions, stems bearing fresh *S. australis* eggs were collected at weekly intervals from two raspberry (*Rubus idaeus* L.) plants in the author's garden from 2.2.80-5.4.80. Every collection time, all egg batches present on the plants were removed so that it was certain, at the next collection time, that batches were less than a week old. The stems, bearing batches, were placed in labelled, 15 cm lengths of transparent 3 cm diameter polythene pipe. Each end was covered with wide meshed gauze held in place with a rubber band and the pipe was placed in a vertical position in an open wooden frame in light shade outdoors. Thus situated, the egg batches were subjected to normal weather conditions including frequent periods of wetting and drying, depending on the rainfall. During spring, the samples were inspected daily from late September to determine when eclosion commmenced.

Results.

The first nymphs hatched on 5.10.80, from the samples consisting of eggs laid prior 2.2.80 and in the week 2-9.2.80. The remaining 6 samples all commenced hatching within 7 days with the last, those eggs laid 29.3.80-5.4.80, hatching on 12.10.80. Thus the egg stage showed considerable synchronisation in hatching with some eggs taking as little as 189 days and others over 245 days to complete development.

2, Duration of the egg stage at various constant temperatures.

Throughout the course of this study, *S. australis* eggs, on a variety of oviposition materials, were maintained at constant temperatures from 4°C - 30°C in the laboratory. The 30, 20, 15, 10 and 4°C incubators varied less than a degree from the temperature required but the 25 and 20 °C growth rooms usually varied by up to 3°C. These pilot tests indicated: eggs in bracken and blackberry suffered high mortality from fungi and an unidentified mite which multiplied prolifically at the higher temperatures; generally the 'cleaner' raspberry canes were better substrates for experimental purposes; the earlier in the season the eggs were collected, the more difficult it was to get satisfactory survival and results. With these prior results in mind, the following experiment was conducted in 1984.

Stems of raspberry, bearing *S. australis* egg batches, were collected from the author's garden on 2.9.84. Approximately equal numbers of egg batches (ca. 2000 eggs) were placed in each of five 250 ml glass jars. A 20 ml glass vial containing water and with a tissue paper wick was included in each jar to maintain a high humidity. Each jar was covered with a plastic screw cap and kept at a constant temperature, either 25, 20, 15, 13 or 10°C. Jars were usually examined daily until eclosion had commenced at 13°C, then at 2 day intervals until emergence had ceased in the 15°C sample. After that, the remaining jars were examined at less regular intervals.

At each examination, nymphs in each jar were counted and removed. Most nymphs gathered on the undersurface of the lid and did not move if the lid was unscrewed carefully. The remaining nymphs in the jar were counted after inverting the jar and giving it a sharp tap. This knocked the remaining nymphs onto the cleaned lid.

Once emergence had ceased and the total number of nymphs per jar determined for each temperature, the cumulative % eclosion was calculated for each examination day. As the emergence pattern for most temperatures was very skewed, the median, rather than the mean day of emergence, was calculated for each temperature and plotted against days from experiment commencement.

Results.

Only a few individuals hatched at 30°C which must therefore be considered very close to the upper lethal limit. Eggs held at 4°C failed to hatch even after long periods but hatched successfully later when placed in warmer temperatures, as long as no desiccation had occurred. The relationship between dates of collection and number of days till initiation of eclosion at 25, 20 and 15°C for eggs collected between 1980-84 are shown in Fig 13:1. Results from the 1984 experiment are also included. Eggs collected before June failed to hatch at 25 and 20°C but hatched if kept at 15°C. The prolonged and slow emergence at 15°C resulted in the initiation of hatching being missed in samples collected early in the season because of the very few individuals involved. Consequently results from only one collection date prior to June could be accurately presented in Fig 13:1 even though eggs collected as early as 14 February hatched successfully at this temperature. The linear regression for each temperature is also presented with June 1 being day 1 for the 25 and 20°C relationship and April 1 for 15°C. The 1984 results show that differences may occur from year to year.

The results of the 2.9.84 hatching experiment are presented in

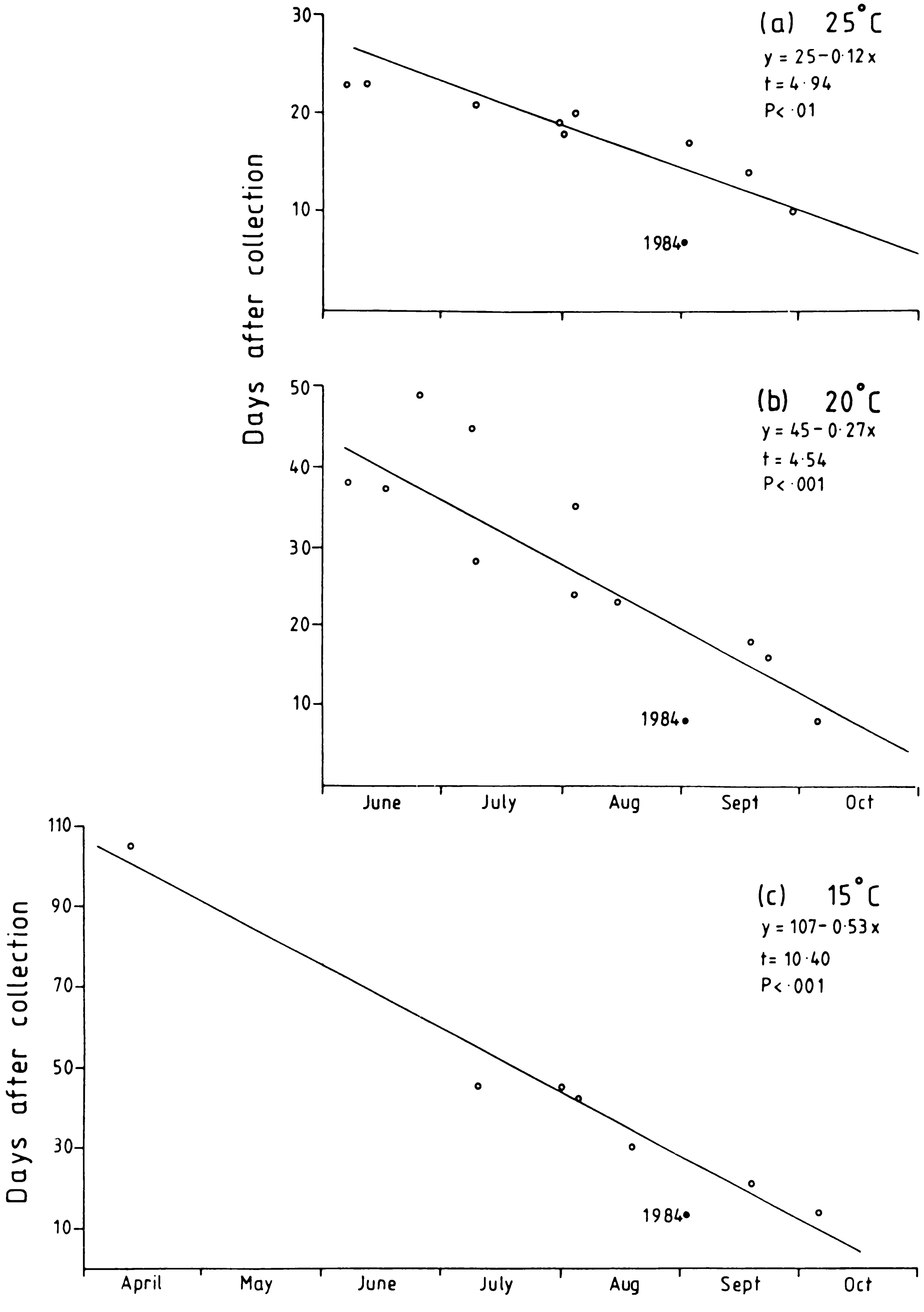


Fig 13:1 Relationship between date of collection and number of days till initiation of egg eclosion of *S. australis* at 25, 20 and 15°C.

Fig 13:2. At 10°C 10 nymphs only were found on the 88th day, only a very small % of the approximately 2000 eggs held at this temperature. The incubator in which they were held had been open for several minutes the previous day when other samples were being sorted and the associated rise in temperature may have initiated the emergence. Embryos at 10°C develop slowly till fully mature, but usually do not hatch until moved to warmer temperatures. The occurrence of this very small % hatching indicates that the lower threshold for *S. australis* egg hatch must be very close to 10°C.

It is apparent from Fig 13:2 that the number of days till commencement and the number of days over which hatching occurs increases as temperatures fall. Eighty percent of eggs had hatched by the third day at 25°C, by the 6th day at 20°C, the 12th day at 15°C and the 38th day at 13°C. Although approximately the same number of egg batches were put into each jar, only 626 nymphs emerged at 25°C, compared with 1359 at 20°C, 1988 at 15°C and 1785 at 13°C, indicating that some mortality was occurring at 25°C.

When the median day of hatching, as well as initial day of hatching, is plotted for each temperature (Fig 13:3) the curves approach an asymptote near 10°C indicating the lower temperature threshold for egg hatch. When the reciprocals of these (i.e. rates) are plotted against temperature, it can be seen that curvilinear relationships exist although between 25, 20 and 15°C the curve is relatively linear.

The linear portion of the rate versus temperature curve is used in day degree models for predicting insect development (Arnold 1960, Baskerville and Emin 1969, Allen 1976) and authors investigating temperature effects on host-parasite relationships have used these models to obtain empirical estimates of threshold temperatures and day

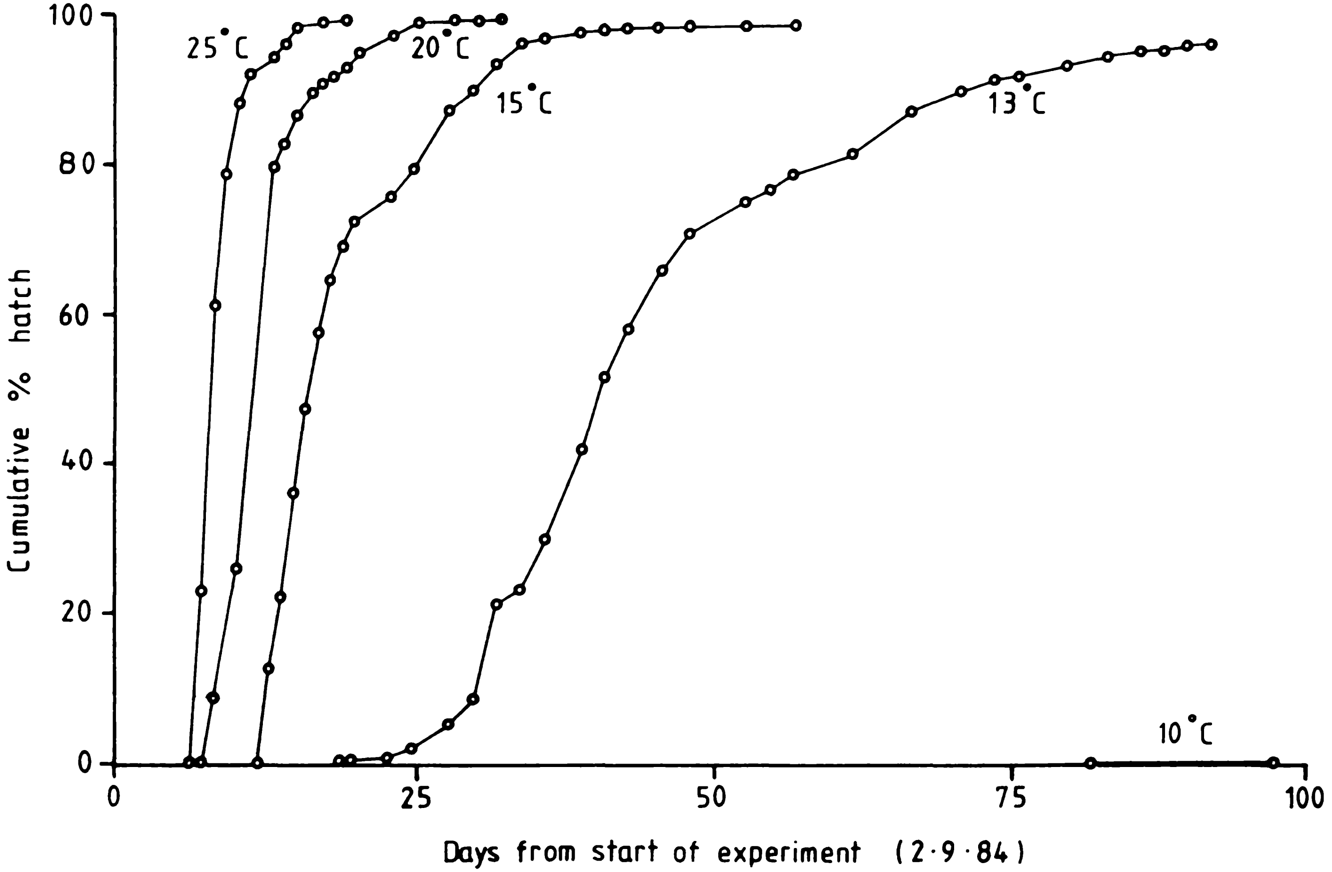


Fig 13:2 Effect of constant temperature on commencement and duration of S. australis egg eclosion.

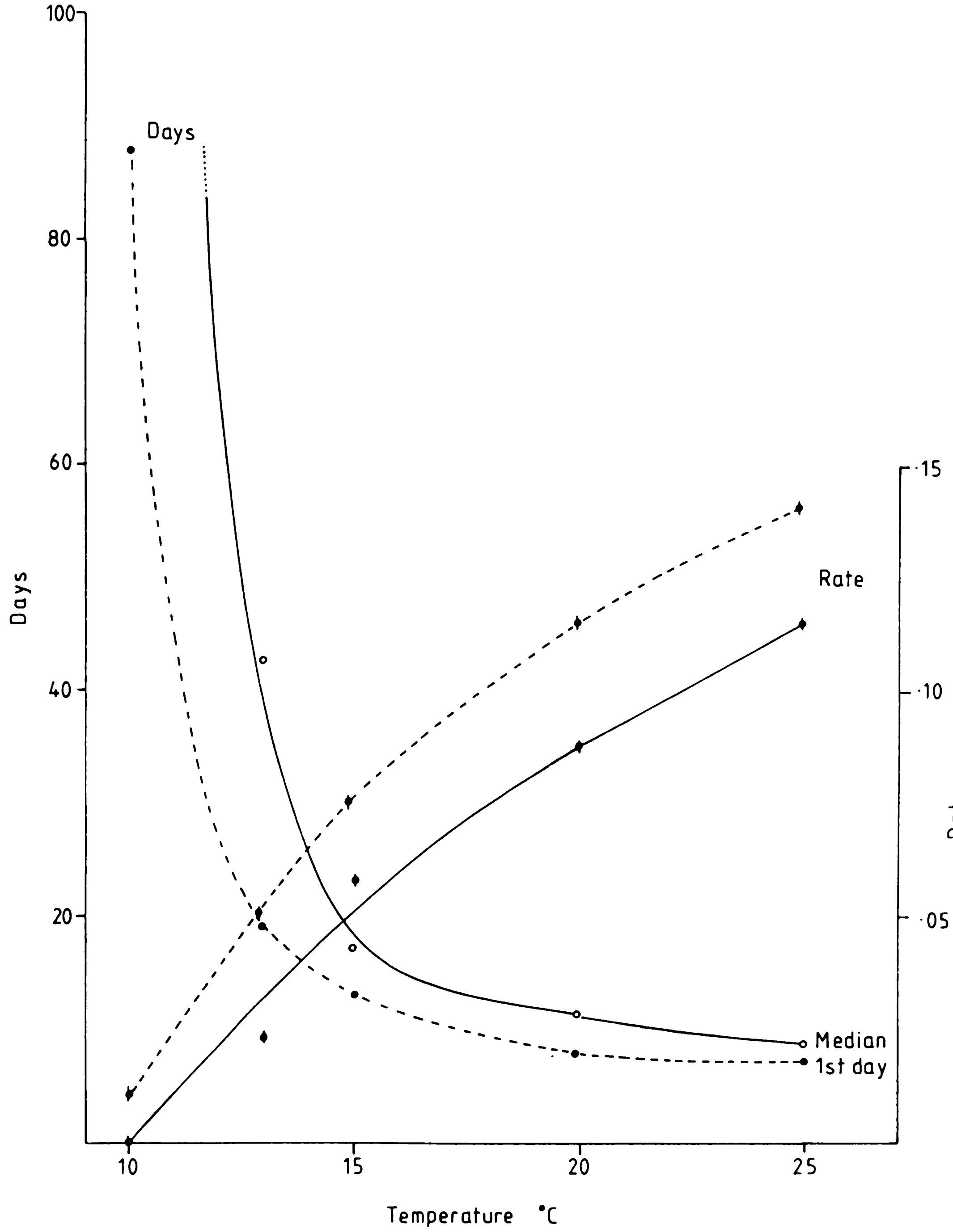


Fig 13:3 Relationship between median and first day of egg eclosion of *S. australis* and temperature (curves drawn by eye).

degree requirements for comparison between species (Campbell et al. 1974, Nealis et al. 19840). However, the 2.9.84 experiment was conducted over only a small proportion of the total egg stage and the data cannot validly be used for prediction of day degree requirements of the whole egg stage.

An estimate of the days required for the completion of the whole egg stage at each temperature can be obtained by extrapolation of the linear regressions in Fig 13:1. April 1st, being at the end of the oviposition period, was chosen as the commencement date. By substituting its corresponding value in the regressions (-61 for 25 and 20°C and 0 for 15°C) the equations give a prediction of the mean number of days required to initiation of hatching for a population of eggs laid on April 1st at each temperature. The estimated standard error for the prediction is

$$S_y = s_{yx}(1/n) + (x_o^2/\Sigma x^2) \qquad \text{with } n-2 \text{ df}$$

when n = number of observations

x_o = predicted x - mean x

s_{yx} = sample standard deviation from regression

By multiplying the predicted days by (temperatures minus the lower temperature threshold for hatching (10°C)), an estimate of the required day degrees at each of the three temperatures can be obtained. Both the predicted days and day degree requirements for 25, 20 and 15°C are presented later in Table 13:1. To allow comparison, these three estimates are repeated for the nymphal and parasite development.

3, Rate of nymphal development at constant temperatures.

S. australis has an extremely wide range of host plants. As host plant can affect rate of development, it was desirable to select a relevant host plant in the following study. Although bracken and blackberry were the main host species in the study area, the growth habit of neither was suitable for small pot experiments in incubators and growth rooms. The host plant chosen was *Passiflora edulis* L., as it was easily grown from seed in pots, was tolerant of growth room conditions, it branched readily providing many possible feeding sites for nymphs and as well, it is the plant from which the Passion vine hopper derives it's common name. Passion vine plants were grown from seed in 15 cm^3 plastic pots, allowing for 6 pots to be used at each temperature (15, 20 and 25°C). Plants were placed close together in the centre of a large tray of water with the pot bases just above water level. This helped maintain a high humidity which was essential for nymphal survival in the growth rooms. Plants were watered as required.

Newly emerged nymphs were obtained from eggs held at a constant temperature of 20°C. Depending on the number available, 20-40 nymphs were placed in 15x12 cm bag-like cages (Fig 13:4). High mortality in the first day or two left 6-12 nymphs per cage. The cages consisted of clear polythene on one side and fine gauze on the other, sewn along the long edges and across one end. The corners were angled to prevent nymphs being trapped and allow a position where a label could be attached. The polythene allowed the developing nymphs to be viewed and helped maintain humidity.

The cage containing the nymphs was slipped over a growing shoot and tied in place with cotton threads remaining at the cage edge after sewing. The placement of neonate nymphs on the plants was staggered

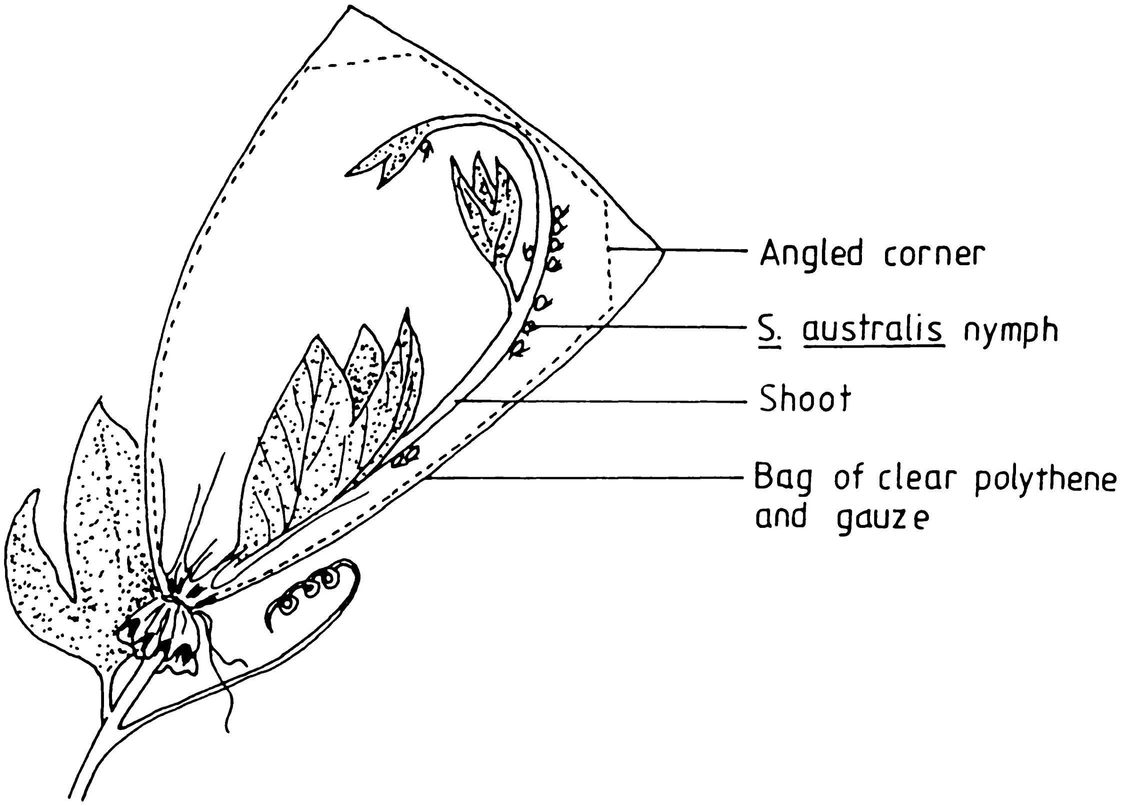


Fig 13:4 Diagram of cage used to enclose *S. australis* nymphs on *P. edulis* shoots.

from 19.7.84 till 19.9.84. This was because of the availability of nymphs but also minimised the affects malfunctions in the growth rooms. Eventually all plants had two cages of nymphs

Cages were checked at weekly intervals and the number of each nymphal instar counted. The m.i. (Chapter 7) of each cage was calculated and the values plotted against number of days from hatch. Once all nymphs had matured or died in each cage, the cage was removed from the plant. Because of time limitations, the 15°C nymphs were not followed to maturity but rather till all had reached the 4th instar.

Results

Fig 13:5a-c shows a wide degree of variability occurs between individual cages in nymphal development. At 25°C in particular, it was noticible that nymphs in exposed cages grew at a slower rate and died more readily than those in the centre of the plant group which were protected from bright light and air currents from the temperature control mechanisms. Some plant shoots were more vigorous than others and had correspondingly better nymphal growth rates. Mortality was high at 25°C and only 2 cages had nymphs reach full maturity.

Linear regression equations can be calculated relating development time and each temperature and, as with the eggs, can be used to predict the average number of days required for a population to reach maturity. The predictions and the associated day degree accumulation for each temperature are presented in Table 13:1.

4, Interpretation of *S. australis* results.

The duration of the *S. australis* egg stage in Hamilton varied

```
        -
days    -                                         2            1
        -                                        11     1
        -                                         2   1
      90+                1                        1
        -                                         3
        -                             1          11
        -                1            1           1
        -                2            1       2
      60+                1   1        2
        -                11       1   1 1
        -                3            2
        -                   1      11
        -                3         1
      30+                4
        -    2 1         2
        -    61
        -    6
        -    3
       0+                                    y = -6•99+23•5x
        -
          +---------+---------+---------+---------+---------+------
       0.80      1.60      2.40      3.20      4.00      4.80
                                     mi
```

Fig 13:5a. *S. australis* nymphal development at 15°C.

Number represents no. observations at any one point.

```
     160+                                                      1
        -                                                   1
days    -                                  1       1         1
        -                                  1    1  1        21
        -                                            2        12
     120+                                       1    2     21 2
        -                                  1         2   1 1 1
        -                                  1         2     1 1
        -                                  2  1   1   1  1
        -                                  1    1 1    1
      80+                        1         3  1    111         1
        -                        1         3  1        1
        -                        2 1     2 12        1
        -                        31        2        1
        -                        5  1    1 2
      40+                11   1112   1
        -          1   1  121  1 1
        -    1        14 1   1
        -    3    1   11
        -    4                                   y = -21•7+24•8x
       0+
         ----+---------+---------+---------+---------+---------+--
            1.0       2.0       3.0       4.0       5.0       6.0
                                     mi
```

Fig 13:5b. *S. australis* nymphal development at 20°C.

Number represents no. observations at any one point.

```
        -                                                      1
days    -
        -                                                 1
        -
      90+
        -                                            1       1 1
        -                             1
        -                                     1        1  1  1
        -                       2                    1 2
      60+                       1            1    1   1
        -                                 2      1  1
        -                       1       1 1
        -                      12         1
        -             1     1   2
      30+             2   1   1
        -   1         3   1     1
        -   1 1 1    32 1
        -   311    21 5
        -   6
       0+                                    y = -8•59+15•8x
        -

          ----+---------+---------+---------+---------+---------+--
             1.0       2.0       3.0       4.0       5.0       6.0
                                      mi
```

Fig 13:5c. *S. australis* nymphal development at 25°C. Number represents no. observations at any one point.

from 189-245 days which is a little longer than the 6 months noted in Australia by Fletcher and Anderson (1980). The long overwintering stage is probably common amongst univoltine Auchenorrhyncha. Waloff (1980) lists 7 grassland species with overwintering egg stages and Claridge and Reynolds (1972) found overwintering *Oncopsis* (Hemiptera:Cicadellidae) eggs present 9-10 months of the year.

Earlier New Zealand authors held that *S. australis* had an obligatory diapause (Siew 1960, Cumber 1966, Matheson 1978) but this was found not to be so by Fletcher and Anderson (1980). Cumber (1966) considered diapause existed because eggs collected prior to the end of June failed to hatch when held at laboratory temperatures. As observed in other leafhoppers (Claridge and Reynolds 1972) *S. australis* eggs show a marked increase in size which occurs at the end of May and early June with length increasing from the newly laid 0•77 - 0•87 mm (Fletcher 1979) to 1•04 ± •06 mm (n = 20). This coincides with the parting of the yolk and appearance of the head lobes of the embryo in the base of the egg prior to the commencement of blastokinesis. This swelling occurs at the same stage of egg development in *Saldula* (Heteroptera : Saldidae) (Cobben 1968). In this study it was found that although eggs laid early in the year hatched when held at 13 and 15°C, it was only after this swelling had occurred that field collected eggs would successfully hatch at 20 and 25°C. Absorption of free water is necessary for embedded eggs of many Miridae and Nabidae (Heteroptera) that swell during development (Cobben 1968). At the lower temperatures, condensation on the jar walls occurred and as the woody oviposition material felt damp, the eggs within presumably could absorb water. At 20 and 25°C, although humidity was high and no desiccation occurred, eggs never came in contact with water in the liquid form. My hypothesis is that absorption of free water is essential just prior to blastokinesis for further egg development to proceed. This would explain Cumber's (1966) and Matheson's (1978) lack of success in hatching early *S. australis* eggs. Attempts to prove this hypothesis failed as fungal growth repeatedly killed sample eggs at the higher temperatures.

If diapause is not responsible for synchronising eclosion as suggested by Cumber (1966) then other factors must play a role. If water is essential at a particular stage of egg development, rainfall or the lack of it, may help close the gap between early and late eggs. Warm temperatures near hatching are important as demonstrated by the high proportion of the total population emerging in the first few days after eclosion commenced at 20 and 25°C (Fig 13:2).

As expected, temperature had a strong influence on the duration of the egg stage. The predicted day degree values in Table 13:1 average around 530 day degrees and there is no conflict with the day degree totals recorded on the site from the end of oviposition in April until the first appearance of nymphs in 3 successive seasons (Table 13:2).

Table 13:2 also shows day degree accumulation for the months after the swelling (June-September). It can be seen that this gives a better indication of whether egg eclosion will be early or late in a particular year than the total day degree accumulation from April 1st.

The day degree estimates for nymph to adult (Table 13:1) are higher in the laboratory than the 900-1000 indicated in the field in Fig 7:7. This could be expected as the laboratory nymphs were caged and could not move freely to the choicest shoots as they would naturally. Also the growth room conditions may not have been optimum for *S. australis* development. As *S. australis* females commence oviposition about two weeks after maturing, adding egg and nymphal

Table 13:1 Day degree requirements for completion of development by *S. australis* and *C. scolypopae* at constant temperatures of 15, 20 and 25°C.

	15°C	20°C	25°C
S. australis			
;egg	543±35	611±78	487±49
;nymph to adult	670±30*	1271±19	1293±41
C. scolypopae			
	1365**	726±26	810±45***

* value from extrapolation of Fig 13:5a

** single observation.

*** individuals reared in dark.

Table 13:2 Date of first appearance of nymphs and day degree (°D) accumulations in the previous months in study area 1982-84.

Date	°D April-Sept	°D June-Sept
23.10.82	491	267
11.10.83	614	317
3.10.84	573	331

day degree requirements would not give the full requirement for a whole generation. Comparison of laboratory and field studies suggest that the total day degree requirement is between 1500 -1900. This requirement would clearly limit *S. australis* distribution in New Zealand as it is equivalent to a mean annual temperature in the range of 14-15°C. This does not conflict with the close correlation noted by Matheson (1978) between Cumber's (1966) map of *S. australis* distribution and the 12°C isotherm of a mean annual temperature (Ward 1976) as in any district, *S. australis* concentrates in warm, sheltered sites. Rather than being restricted by the influence of the cold winter temperatures on the egg stage as suggested by (Cumber 1966), the distribution of *S. australis* in New Zealand is the reflection of the temperature requirements for the completion of its whole life cycle.

II INVESTIGATIONS ON THE DEVELOPMENT OF CENTRODORA SCOLYPOPAE

In the study area, *C. scolypopae* adults are present from early February till the start of April. During this time, there is rapid development of the egg and early instars so that most individuals are mature 3rd instars in May and are in the overwintering, barred prepupal stage by June. Pupae are not found till the begining of January, the following year.

1. Effect of constant temperature on development of *C. scolypopae*.

Fresh *S. australis* eggs were exposed to newly emerged *C. scolypopae* adults for 24 hours (1-2 egg batches/female). The host eggs were then removed and placed in labelled 10 ml glass vials. The open vials were then placed in growth jars as described in Chapter 9. The jars were put in incubators at constant temperatures of 10, 13, 15, 20 and 25°C, mostly with a 16 hour light per day photoperiod. Some of those laid between 15-22.5.84, were reared in complete darkness at 20 and 25°C to investigate the effect of light. To ascertain the commencement and possible duration of each stage, host eggs were removed at intervals and parasitised eggs dissected out of the wood. The egg chorion was cleared with 70% ethanol so that thee stage of parasite development could be determined. Closer examination was sometimes needed, in which case the egg was dissected in insect Ringer's solution. The stage of parasite development was recorded, as was the day when any adult emergence was first observed.

Results

Much difficulty was encountered in providing optimum conditions for parasite growth. Host eggs laid in raspberry canes were least prone to fungal attack but the egg depth resulted in low parasitism levels. Passion vine tendrils were readily accepted by both host and parasite but eggs were extremely susceptible to fungal attack. Bracken was a good compromise and dipping it in 5% sodium hypochlorite solution after parasite oviposition helped lessen fungal attack although the unidentified mite species still gave problems.

As parasitised eggs were usually destroyed during the inspection procedure, only 2-4 were taken from each sample batch at inspection. This method of assessment precluded statistical analysis for individual dates but allowed good graphical representation of parasite development. The stage of parasite development at each inspection time for 25, 20, 15, and 13°C is given in Fig 13:6. The development of the early instars was rapid at the higher temperatures and few observations

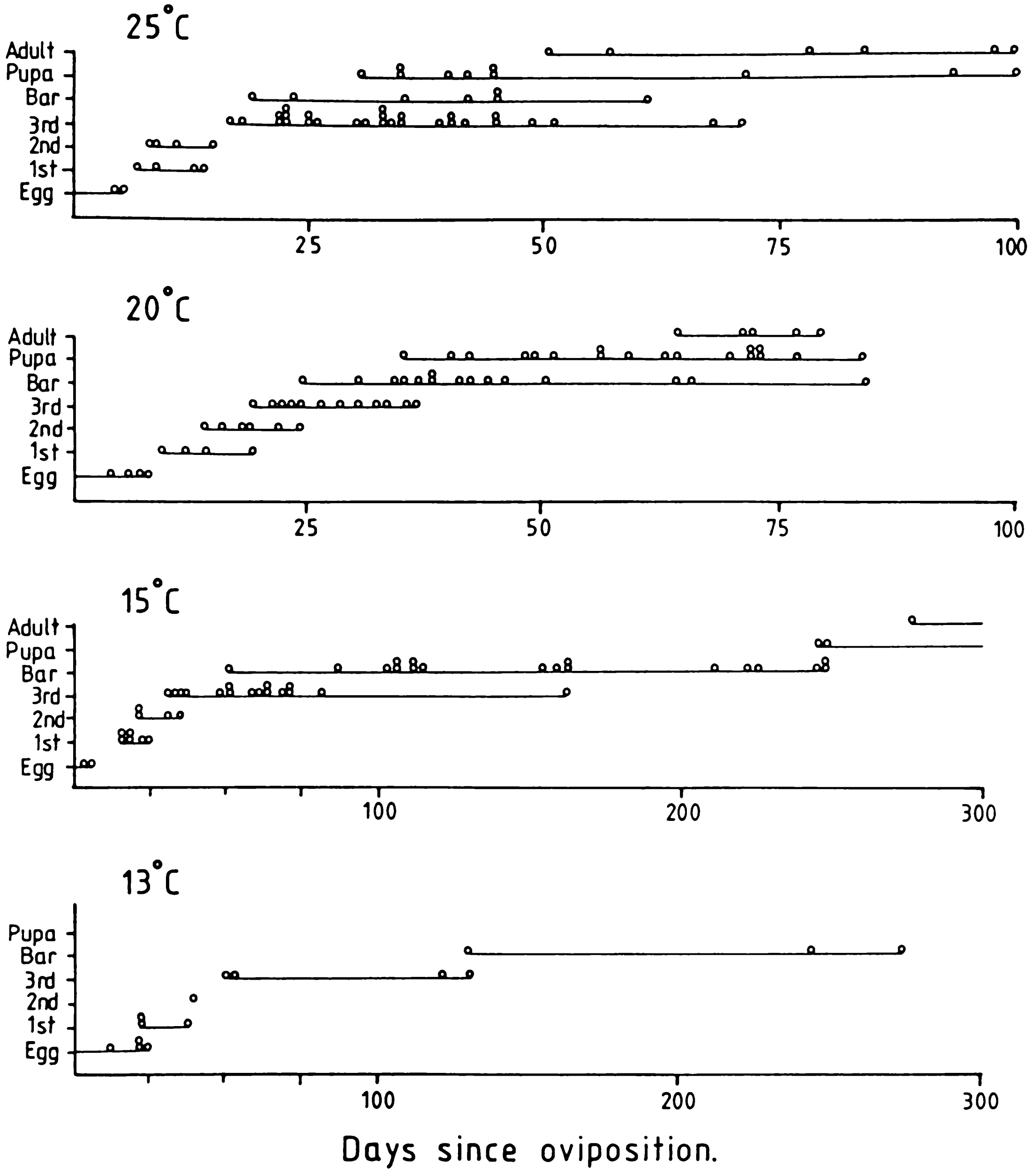


Fig 13:6 Stage of *C. scolypopae* development at inspection times when held at 13, 15, 20 and 25°C. (Each o represents 1 observation day).

were recorded of the 1st and 2nd instars at 25°C. No stage earlier than 3rd instar was found after ~15 days. This transition took proportionally longer as temperature decreased. The later developmental stages all covered protracted periods relative to the 1st and 2nd instars and the pupal stage took about the same time as all prior development. The first adults at 25 and 20°C were found after 50 and 66 days respectively. At 15°C, the barred prepupal stage prior to pupation was present for about 200 days. It is thought that these larvae passed some of this time in a period of arrested development or diapause. Adults were only found in one sample. These sample eggs were laid on 12.4.83 and the first adults emerged 273 days later on 14.1.84, a few weeks prior to field emergence.

Conflicting results appeared when parasite larvae were reared in complete darkness compared to others reared under light (Table 13:3). Even though the sample size was small due to random differences in parasitism between batches (2-16 parasitised eggs), it is clear that at 20°C pupation was inhibited and presumably diapause initiated when parasites were reared in complete darkness. Even after 100 days, the 21 parasitised eggs in the two samples examined examined showed no signs of pupation yet still appeared healthy, indicating that light plays a role in the initiation of diapause. At 25°C, however, opposite results were obtained. Pupation occurred in 14 out of 16 parasitised eggs in dark conditions but of those in the light, 24 out of 26 inspected did not have the bar that indicates the prepupal stage. All through 1984 difficulty was encountered in rearing parasites from eggs at 25°C while there had seemed little difficulty the previous year in a different growth room. It is possible, in retrospect, that the more intense light in the 1984 room may have been too bright for optimum growth of young larvae.

Table 13:3 Effect of presence or absence of light on initiation of diapause of *C. scolypopae* reared at 20 and 25°C.

	16 hours light		No light	
	days since oviposition	% pupation	days since oviposition	% pupation
	35	100	56	0
	40	100	57	0
	42	100	58	0
20°C	44	100	61	0
	63	100	62	0
	64	50	106	0
	72	25	108	0
	78	100		
	34	0	34	50
25°C	35	0	35	100
	40	0	40	100

Adult emergence data was insufficient to calculate a rate-temperature regression and thermal constant (Day degree requirement) for completion of development, as done for other parasite species (Rosen and Eliraz 1978, Nealis et al 1984). However, by plotting the reciprocals of the first appearance of each stage at each temperature, much can still be learnt of the relationship between the parasite's development and temperature. From Fig 13:7 we can see that the lower temperature for hatching is at least 10°C. No eggs showed any development at this temperature. The 2nd, 3rd and barred prepupal stage show a threshold between 10 and 12.5°C and that for the pupal and adult stage is even higher at around 14.5°C.

To obtain some idea of the thermal requirements of *C. scolypopae* and allow comparison with *S. australis*, the number of days recorded till the first appearance of adults at each of the 3 temperatures was multiplied by the temperature minus 10°C, the approximate lower threshold for *C. scolypopae* egg hatch. Because of the occurrence of diapause at 15°C, the day degrees estimate at that temperature is much higher than for the other two temperatures. Values are given in Table 13:1.

2, <u>Initiation and completion of diapause in the field</u>.

During 1983, it was noted that parasites collected in the field from July onwards and exposed to long photoperiods in the laboratory took longer to pupate than those collected before this month. This was thought to have been caused by the onset of diapause. To investigate the changes in intensity of diapause, parasitised *S. australis* eggs were collected at intervals from March to December from the study site in 1984. They were placed in the previously described growth jars and

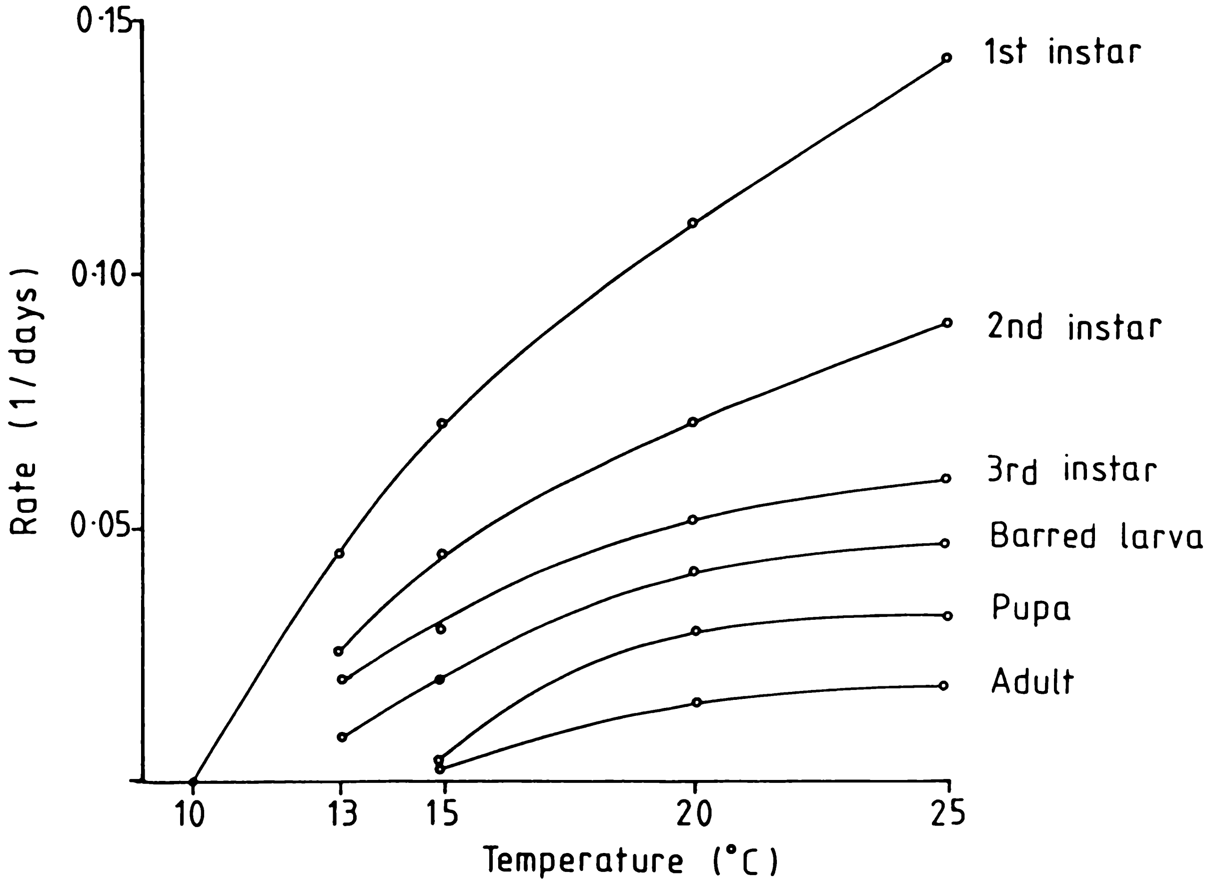


Fig 13:7 Rate of *C. scolypopae* development at constant temperature. Curves fitted by eye.

exposed to 16 hours light per day at 20 or 25°C. Eggs were inspected at weekly intervals to determine the time of initiation of pupation and emergence of adults.

A second set of experiments examined the effect of light and dark on overwintering eggs. In 1983, it had been found that by covering eggs collected on 31.7.83 with black polythene, pupation had not occurred in the 30 parasitised eggs examined 28 days later even though most parasites had pupated in the sample collected the same day and exposed to a long photoperiod. This was repeated in 1984 with samples collected on 14.10.84 and 1.11.84. Each time the material was divided between two growth jars. One was wrapped in black polythene and, in case the plastic absorbed heat, the jar was then placed in a white cardboard box. Both jars were then placed in the 25°C growth room where the uncovered eggs were exposed to 16 hours light per day. Both sets of jars were inspected about 40 days after the collection dates, on 27.11.84 for the first jars and 9.12.84 for the second jars. Twenty egg batches from each jar were examined for any sign of pupation (presence of meconial pellets was taken as commencement of pupation) and the number of parasitised eggs containing pupae or no pupae counted.

Results

The long duration of the first experiments in particular meant that the author was occasionally absent from Hamilton at the weekly inspection dates. The results are of the first time of observation and thus, in some cases, are overestimates of the time required for pupation and emergence. Table 13:4 shows the results from both 1983 and 1984 presented in order of calendar month. It can be seen that

Table 13:4 Days till first pupation and adult emergence of field samples collected 1983-84 and held at constant temperature and 16 hours light per day. (ns = no sample)

Collection date	25°C		20°C	
	pupae	adult	pupae	adult
17.2.83	37	ns	ns	ns
25.3.84	ns	32	ns	ns
3.5.84	13	13	ns	ns
24.5.84	ns	ns	47	105
10.6.84	ns	ns	87	94
7.6.83	ns	31	ns	ns
12.6.83	18	37	ns	ns
3.7.84	37	60	98	ns
5.7.83	ns	ns	62	ns
9.7.83	21	55	ns	ns
29.7.84	ns	42	74	81
31.7.83	24	ns	ns	ns
4.8.83	ns	ns	77	103
18.8.83	42	63	82	ns
2.9.84	34	41	58	88
18.9.83	32	ns	ns	ns
3.9.83	33	56	ns	ns
14.10.84	ns	44	44	ns
1.11.84	30	39	33	ns
8.11.83	28	ns	ns	ns
3.12.84	13	ns	26	ns
6.12.83	11	ns	11	63
4.1.83	13	ns	ns	ns

adult emergence occurs within 33 days at 25°C in the samples collected up to early June. These included the February and March samples which were still eggs or 1st and 2nd instar larvae respectively at the time of collection. Samples collected in May and June contained mature 3rd instar or prepupal larvae. From July onwards, even though all parasites had reached the barred prepupal stage and could be expected to pupate within a week or two if reared at constant temperature, the field collected larvae took 6-9 weeks to emerge at 25°C. It is not until December that the time till pupation and emergence noticibly shortens. Parasites held at 20°C appear to take almost twice as long as those at 25°C to pupate. This is a far wider margin than occurs when reared from eggs and as the photoperiod was the same, indicates that the high temperature may aid the termination of diapause.

Results of the light and dark experiment are shown in Table 13:5. Samples collected on 14.10.84 behaved the same as those from 1983, with much pupation occurring in the parasites exposed to light but little in those held in the dark. However, the samples collected 1.11.84 showed no difference between light and dark regimes. It can be inferred from the 14.10.84 results, which repeated the 1983 test, that photoperiod aids in the termination of diapause in the laboratory.

3, Observations of *C. scolypopae* in the field.

Pupation at the study site commenced in January, the earliest date recorded being 4.1.82 and the latest 11-18.1.83. A malaise trap was set up to monitor adult activity. The numbers trapped were low. A summary of the results are given in Table 13:6.

Larval development was rapid, especially in 1981 when the barred stage was present by 25.3.81. This contrasted with 1983 when on

Table 13:5. Pupation of *C. scolypopae* held at 25°C in 16 hours light per day or complete darkness.

		No. pupated	No. not pupated	Mean % pupation ± s.e.
14.10.84	dark	12	139	7•1 ± 3•4
	light	133	3	98•4 ± 0•2
1.11.84	dark	84	12	85•8 ± 6•4
	light	64	20	75•6 ± 6•4

Table 13:6. Dates of first, peak and last catches of *C. scolypopae* adults in a malaise trap. Block AB 1981-84

Date	First catch	peak catch	last catch
1981	(100% emerged by 12.2.81)		23.3.81
1982	23-31.1.82	21-27.2.82	14.3-3.4.82
1983	20.2-3.3.83	3.3-6.3.83	4-14.4.83
1984	16.2.83	1-13.3.84	1.4.84

2.4.83, unhatched parasite eggs were still to be found and the largest larvae were 3rd instars only 2/3 of the host in length.

During the 1981 egg mortality samplings evidence was found that the diapause in *C. scolypopae* is facultative (Table 13:7). A high proportion of parasites in blocks AT and AB had pupated by the time of the May sampling (6-19.5.81) but no adults had emerged. The October sample revealed that some emergence did eventuate but as the malaise trap had been dismantled in mid April, no evidence of when this emergence occurred was obtained. The levels of pupation did not differ between the May and October samplings (t=0•641) so the sample results were combined.

Table 13:7. Percentages of 1981 *C. scolypopae* population pupating and emerging in the same year.

Block	% pupation	% emerged
AT	59•9 ± 3•5	34•6 ± 5•7
AB	31•0 ± 5•1	8•3 ± 3•4
BT	9•9 ± 4•0	1•0 ± 1•0
BB	10•2 ± 2•3	1•9 ± 1•0

Table 13:7 shows that about 60% of parasites in Block AT pupated and about half of these emerged. In other blocks, most premature pupae failed to mature and died. The distribution of pupating individuals between blocks follows the same pattern found with the m.i. values of *S. australis* nymphs in Chapter 7 and is likely to be a similar response to the higher temperatures on site A.

Premature pupation levels in subsequent years were insignificant with only 3 pupae being found in 1982, none in 1983 and 4 in 1984

(Block AT missing) out of the thousands of eggs inspected in the course of the egg mortality samplings. The large number of individuals not entering diapause in 1981 appears to be a response to the warm temperatures experienced that year. The day degree summations (10°C lower threshold) for the months of most *C. scolypopae* developmental activity (January, February and March) using Rukuhia data were 807 in 1981, 697 in 1982, 609 in 1983 and 676 in 1984.

III SYNCHRONISATION OF DEVELOPMENT BETWEEN PARASITE AND HOST

Most Aphelinidae are parasites of multivoltine hosts and in the field, at least in spring and summer, have a short life cycle (15-35 days) and several generations per year (Viggiani 1984). Apart from *C. scolypopae*, only one other aphelinid, *Azotus pulcherrimus* (Merc.), has been recorded having a single generation in a univoltine host. *A. pulcherrimus*, is an Italian primary egg parasite of *Hysteropterum flavescens* (Oliv.) (Homoptera : Issidae) and appears very similar to *C. scolypopae* with adults appearing at mid summer, larval development completed within two months and overwintering in a state of diapause, although as pupae (Viggiani 1973).

The duration of the life cycle of *C. scolypopae* at constant temperatures of 20 and 25°C is a little longer than those recorded for other Aphelinidae. For example, *Aphytis chilensis* Howard, which is slower than other members of the genus, takes 45-61 days at 19°C and 24-30 days at 24°C (Rosen and Eliraz 1978). That the pupal stage lasts about the same duration as all the larval stages (Fig 13:6) is typical of Aphelinidae (Viggiani 1984) and differing lower thresholds for different developmental stages has also been previously recorded, eg in *Aphelinus mali* Haldeman, it is 6-7°C for larvae, 13°C for pupae and

15-16°C for the adult (Bonnemaison 1965).

In field conditions, diapause enables *C. scolypopae* to synchronise adult emergence with the oviposition period of*S. australis* and to enhance survival over unfavourable winter conditions. Diapause in endoparasitic Hymenoptera is controlled by photoperiodic stimuli (Fisher 1971). In some it is the maternal generation that receives the stimulus as in *Mormoniella vitripennis* (Pteromalidae) (Schneiderman and Horwitz 1958). In others, such as the egg parasite *Caraphractus cinctus* (Mymaridae) it is the prepupae (Jackson 1963). *C. scolypopae* appears to be one of the latter, even though the parasites are buried within woody tissue.

It is apparent that the initiation of diapause in *C. scolypopae* is influenced by both temperature and light. Diapause occurs at 15°C in spite of a long photoperiod. At 20°C, those without light enter diapause but those exposed to long photoperiod continue development. At 25°C, diapause does not occur in individuals kept in complete darkness.

Once started, overwintering diapause is maintained by a low temperature threshold and/or short day lengths. As the season progresses, diapause intensity decreases and normally diapause ends after the winter solstice without a specific stimulus. Subsequent development is dependent on the occurrence of physical conditions favourable for growth (Tauber and Tauber 1976).

For insects with a photoperiodically determined diapause, the diapause is considered terminated when field samples in diapause maintaining and diapause terminating photoperiods show equivalent degrees of development. Table 13:5 showed that the 14.10.84 sample held at 25°C in darkness did not come out of diapause as soon as that in the long photoperiod but the 1.11.84 samples showed no such difference, suggesting that diapause ended in the latter half of October. The results are not conclusive as periodic field samples should be tested over a wide range of photoperiodic regimes, including naturally changing daylengths which can have a significant influence on diapause maintenance (Tauber and Tauber 1976). Such tests were not possible with the facilities available.

The ending of diapause in October coincides with the eclosion of host eggs. Subsequent *C. scolypopae* development is most likely highly dependent on temperature, with the margin between the lower threshold for parasite pupation and adult emergence and that for *S. australis* development, synchronising the appearance of *C. scolypopae* adults and host eggs. The resulting generation of parasite larvae grow rapidly and reach the barred prepupal stage during late April and May, when mean daily temperatures fall below 15°C. The lower low thresholds for *C. scolypopae* egg and larval development allow development to continue till larvae are mature but pupation, with its low threshold near 15°C, is inhibited. Thus the combination of autumn temperature and daylength ensures the initiation of diapause.

In most years this results in one generation well synchronised with the host even when host development was late such as in 1983. The exception was the 1981 population which demonstrated that diapause was facultative. This summer was much hotter than all other years in the study. On the sunny A side of the gully, many new generation larvae reached the prepupal stage before the end of March and failed to enter diapause. About half of these emerged as adults in block AT but no sign of a second generation could be detected at the October sampling. Laboratory tests have shown that *C. scolypopae* can successfully oviposit in eggs of any age, and large 3rd instars have been dissected out of mature *S. australis* embryos. However the mean monthly temperatures for June and July that year were below the lower threshold for egg hatch and it is doubtful that any second generation individuals eventuated. With the high levels of parasitism already occurring that year and the likelihood of superparasitism (Chapter 12) these nondiapausing individuals would contribute little to the following generation.

Many warmer areas in New Zealand would have two complete *C. scolypopae* generations every year. In early March 1982, host eggs collected from around Lake Taharoa, about 35 km north of Dargaville, contained eggs, pupae and adults about to emerge. Samples collected at Flagstaff Hill, Russell, about the same time also contained pupae. Mild temperatures in the following month would enable 2nd generation larvae to reach the overwintering stage easily. However the facultative nature of the diapause results in population mortality in marginal areas, such as the study site and does not aid the stability of the host- parasite relationship.

CHAPTER FOURTEEN

POPULATION DYNAMICS OF CENTRODORA SCOLYPOPAE

Studies of the dynamics of insect populations are often concerned with the interaction between a host and its parasite. However, although life tables may be constructed and analysed for the host population, only rarely are the population dynamics of the parasite studied. Instead most research on parasite populations has been concerned with the modelling of host-parasite interactions. Modern analytical models are framed in difference equations based on those from the early work of Thompson (1924), Nicholson (1933) and Nicholson and Bailey (1935) and are reviewed by Hassell and Waage (1984). The basic form of the equations are

$$N_{t+1} = FN_t \; f(N_tP_t)$$

$$P_{t+1} = cN_t(1-f(N_tP_t))$$

The variables N and P respectively denote population numbers of host and parasite in the t=1 generation. The proportion of the host surviving parasitism is $f(N_tP_t)$ and this function contains all aspects of attack behaviour. F is the intrinsic rate of host increase. The constant c is the number of parasites produced per host attacked.

Many models have been produced for each part of the equations. Ecologists have used simple models to examine the influence of changes in factors on populations, such as multiple species interactions (May and Hassell 1981), prey distibution (Hassell and May 1974) and searching efficieny (Watt 1959, Rogers 1972, Beddington 1975, Rogers and Hassell 1974). The major goal of this work was to discover underlying ecological principles, rather than to model actual populations. However, mathematical theories have outstripped the aquisition of biological data with which to test them. Consequently many population ecologists are resorting to the re-analysis of existing data to verify new models (eg Hassell and Varley 1969, Rogers 1972, Podoler and Rogers 1975, Royama 1984). Therefore, detailed studies of a wide number of natural or 'artificial' host-parasite interactions arising from successful biological control programmes are essential for the greater understanding of the underlying mechanisms involved. Without these, the development of meaningful models and the resolving of debated ecological issues will be inhibited.

Two species host-parasite interactions are not common in nature (Hassell and Waage 1984) and parasite communities are often very complex, forming a web of potential host-parasite interactions (eg Force 1974, Viggiani 1984). The interaction between *Scolypopa australis* and *Centrodora scolypopae*, made even simpler since both are univoltine in the study area, provides a rare opportunity to obtain fundamental information on a natural host-parasite system.

The analysis of the population dynamics of *S. australis* revealed that parasitism by *C. scolypopae* was the key factor determining population change from generation to generation and a delayed density dependent relationship between the two species was indicated.

Data obtained in the *S. australis* egg sampling provided estimates of the larval density of *C. scolypopae*. Combined with information gathered during biological studies of the parasite, it was possible to make a partial analysis of the population dynamics of *C. scolypopae* itself even though errors associated with the population estimates were high.

I POPULATION DATA

Census data was obtained for 4 complete generations of the *C. scolypopae* population from 1981-1984 inclusive (Table 14:1). For simplicity, population estimates are for females only as all parasitised host eggs contain one female but males may or may not be present. *C. scolypopae* larval density was obtained by multiplying the *S. australis* egg population estimates (Chapter 5) by the proportion found parasitised in the egg mortality estimates (Chapter 6). As all parasitism had ceased and no host emergence had commenced, percent parasitism at the sampling times was a true estimate of parasite population (Van Driesche 1983). Thus parasite population estimates were obtained for October 1980, June 1981 and June and October from 1982-84 (Appendix 21). The estimates used in Table 14:1 are pooled data from all blocks although Block AT had to be excluded after mid 1983 when it was destroyed by cattle.

Estimates of the number of parasite eggs laid in host eggs in bracken in 1983 and 1984 were obtained from the superparasitism data (Chapter 12) and for 1981, from host egg samples stored at 4°C in plastic bags and examined in 1984. Although desiccation prevented larvae being counted, oviposition holes were easily seen. One female egg was assumed to have been laid at each oviposition, thus the number of female parasite eggs laid was estimated for each block by multiplying the number of parasitised eggs in June by the mean number of oviposition holes per parasitised host egg (Appendix 21). Eggs on blackberry were examined in 1984. The mean number of holes/parasitised egg was found to be 85-90% of that occurring in 'bracken' eggs in the same block. So that some assessment of total *C. scolypopae* eggs laid in other years could be obtained, the assumption was made that the mean number of oviposition holes/parasitised egg in blackberry was 85% of that found in bracken in the same block. Because host eggs in blackberry are not as susceptible to parasitism, blackberry carries only a small proportion of the total parasite population and thus the errors associated with this assumption would not greatly influence the overall findings. The bracken and blackberry estimates were then added to obtain total block estimates (Appendix 21), then the pooled site mean was estimated, weighted to compensate for the varying block sizes (Table 14.1).

Table 14:1 Census data of *C. scolypopae* in study site, Rukuhia 1981-1984. Population densities expressed as nos./m^2

Stage	1981	1982	1983	1984
Potential eggs	139968	81108*	137808	40954
No. eggs	5691	-	8250	4916
June larvae	4960	7826	5230	3597
Diapausing larvae	3755	7826	5230	3597
October larvae	-	6380	1896	855

* Diapausing larvae used in estimate

C. scolypopae was regarded as univoltine in the study area and individuals that failed to enter diapause in 1981 were regarded as losses, since there was no evidence that they survived to reproduce. This mortality was calculated by multiplying the June block densities by the proportion pupated, then estimating the weighted mean for the site.

Fecundity was estimated by dissecting females reared from oviposition material collected from the site. In 1983 mean fecundity was 31•6±0•8 (n=41) and in 1984, 34•0 ±1•0 (n=22). The superparasitism study (Chapter 12) revealed that the mean number of parasite larvae per host egg determined from singly parasitised eggs gave a direct estimate of sex ratio. The mean larvae/egg estimates were 1•65 in 1983 and 1•60 in 1984, giving female:male ratios of 1:0•65 and 1:0•60 respectively. The difference in these sex ratios was not statistically significant and was thought unlikely to contribute significantly to *C. scolypopae* population dynamics.

No direct estimate was made of the numbers of emerged adults, therefore the number of parasitised eggs in October in the previous host generation was taken as an estimate of emerging *C. scolypopae* females (P_n). The maximum possible number of female eggs laid was estimated by multiplying P_n by the fecundity (34•0) divided by the mean number of eggs laid per host egg (1•60). Both 1984 fecundity and sex ratio figures were used to give maximum possible females. No October 1981 population estimates were possible and the June larval estimate had to be used for P_n in the next generation.

II CONSTRUCTION AND ANALYSIS OF LIFE TABLES

Life tables were constructed for each of the 4 generations and analysed by the methods of Varley and Gradwell (1960). The 1983 life table is presented as an example to show the stages assessed and the derivation of the k values (Table 14:2).

A variance/covariance matrix of the k values (Smith 1973) was constructed to obtain further information. The density dependence of the mortality factors was tested by the method of Varley and Gradwell (1968) in which the regression of each k factor on the log density of

Table 14:2 Life table for 1983 *C. scolypopae* generation.

Stage	No/m^2(N)	log.N	k
Potential eggs	137808	5·139	
		k_1 (variation in natality)	1·223
Eggs laid	8250	3·916	
		k_2 (superparasitism loss)	0·197
June larvae	5230	3·719	
		k_3 (diapause failure)	0·0
Diapausing larvae	5230	3·719	
		k_4 (winter mortality)	0·441
October larvae	1896	3·278	
			K = 1·861

(k_1 also contains pupal and adult mortality from previous year) numbers entering a stage was calculated. Where a significant regression was obtained, the log of the initial density was plotted against the density of the survivors after k and vice versa. If both lines lie on the same side of unity and differ significantly from 1, then the relationship is density dependent.

The use of individual block values was not considered in the analysis of *S. australis* population dynamics because of the ease of movement between them by the later instars and adults. However the small size and use of running as the predominant method of movement by *C. scolypopae* adults, would limit between block migration. Thus blocks can be regarded as separate entities and have been used in some cases where, because of the few generations studied, analysis was otherwise impossible.

III RESULTS

1. Life table analysis

The variation in density of *C. scolypopae* (June larvae) and available hosts (*S. australis* eggs in June) over the study period is shown in Fig 14:1. Peak numbers of both occurred in 1982 and the lowest numbers in 1984.

In 1982, which happened to be the year of peak *S. australis* egg numbers, k_2 (loss through superparasitism) was combined with k_1 (pupal and adult mortality and variation in natality) as superparasitism was not studied that year. However, it was found by using block data from the other 3 years, that although k_2 was independent of either density of available host or parasite density (P_n), it was inversely dependent on available hosts/P_n ($t=2{\cdot}453$ $P<{\cdot}05$) (Fig 14:2). This indicated that

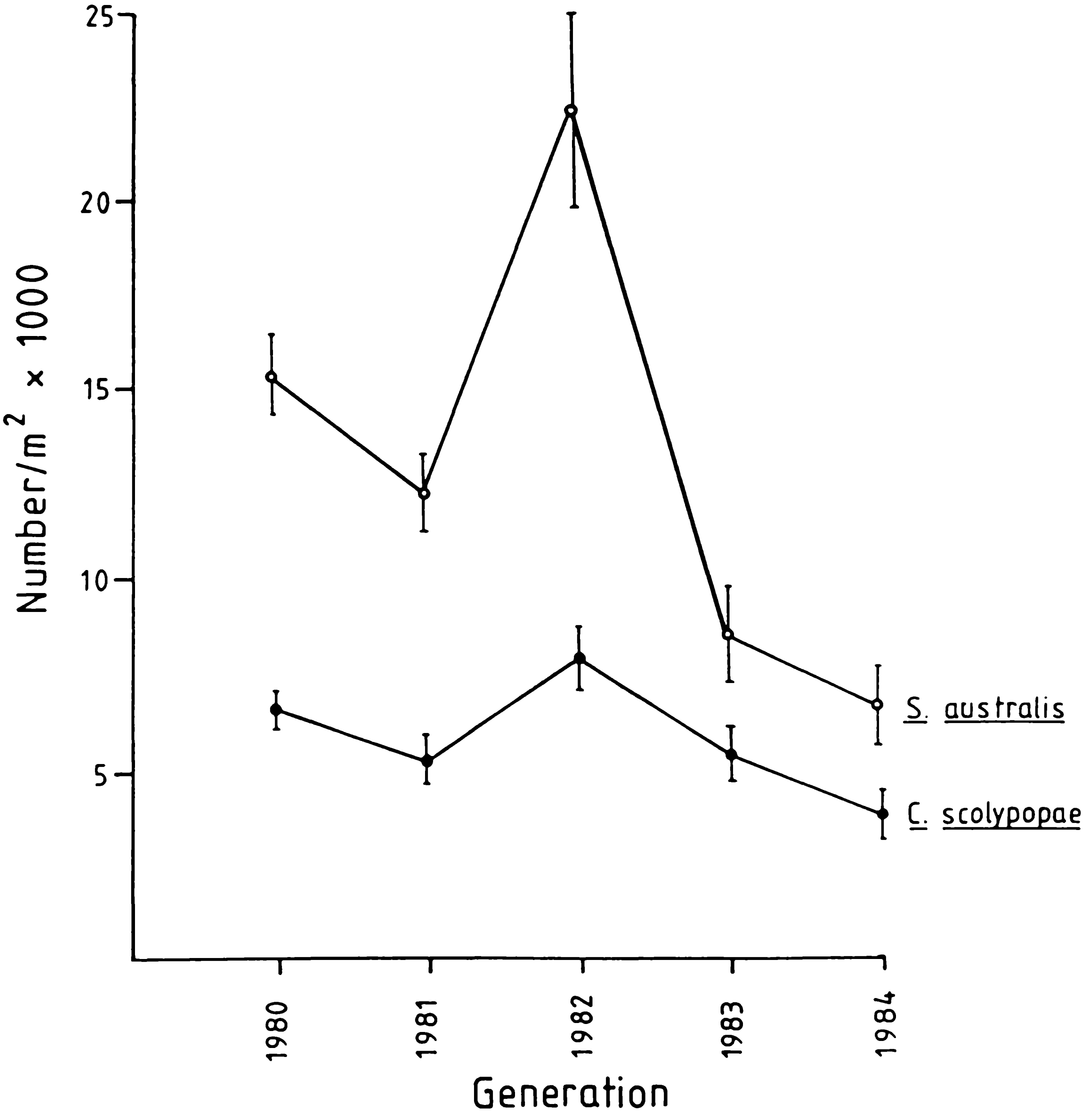


Fig 14:1 Density of *S. australis* eggs and *C. scolypopae*, 1980-84.

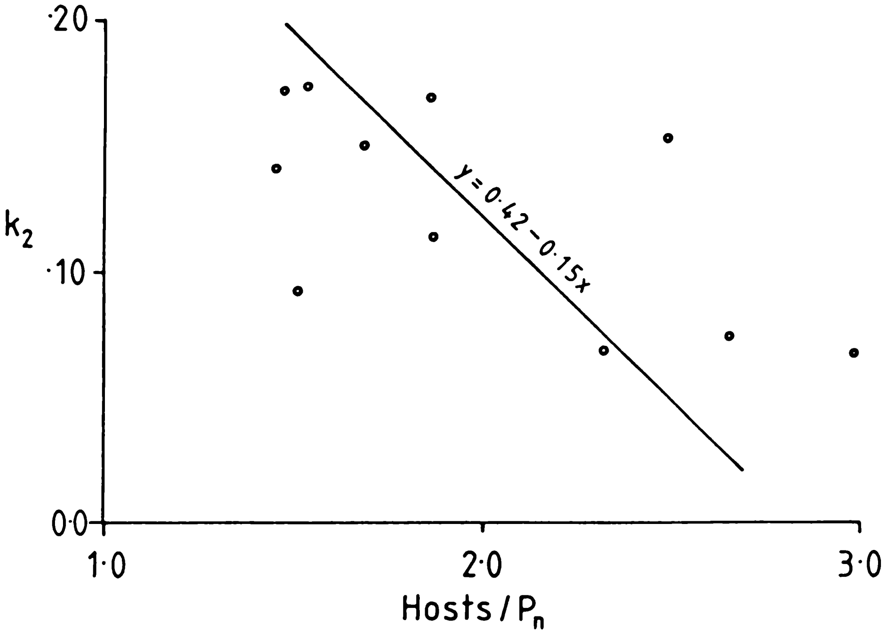


Fig 14:2 Relationship of k_2 (superparasitism) to number of available hosts per searching parasite (P_n).

as available host eggs per parasite decreased, the incidence of superparasitism increased. From the linear relationship obtained, it is possible to obtain an estimate of k_2 in 1982, using the pooled host and parasite population estimates from that year. This value and the k_1 value obtained by subtracting k_2 from the combined estimate, have been used in subsequent k factor analysis. As winter mortality was not estimated in 1981, it is included in the 1982 k_1.

Visual correlation of k factors with K did not reveal an obvious single key factor (Fig 14:3). The largest k factor was k_1 and it contributed much to K. This was not unexpected since it consists of pupal and adult mortality as well as natality loss. It is interesting to note that total K in 1982 is less than all other years in spite of containing winter mortality from the previous year and thus being an overestimate and that of 1981 an underestimate. The variance covariance matrix revealed that k_4 (winter mortality) was the key factor (Table 14:3).

Table 14:3 Variance/covariance matrix for k values and total k

	k_1	k_2	k_3	k_4	K
k_1	·046				
k_2	·001	·007			
k_3	·010	-·002	·003		
k_4	-·035	·019	-·011	·086	
K	·022	·024	·001	·058	·106

The absence of a winter mortality assessment in 1981 was thought to have possibly caused a spurious result (it had been given a value of

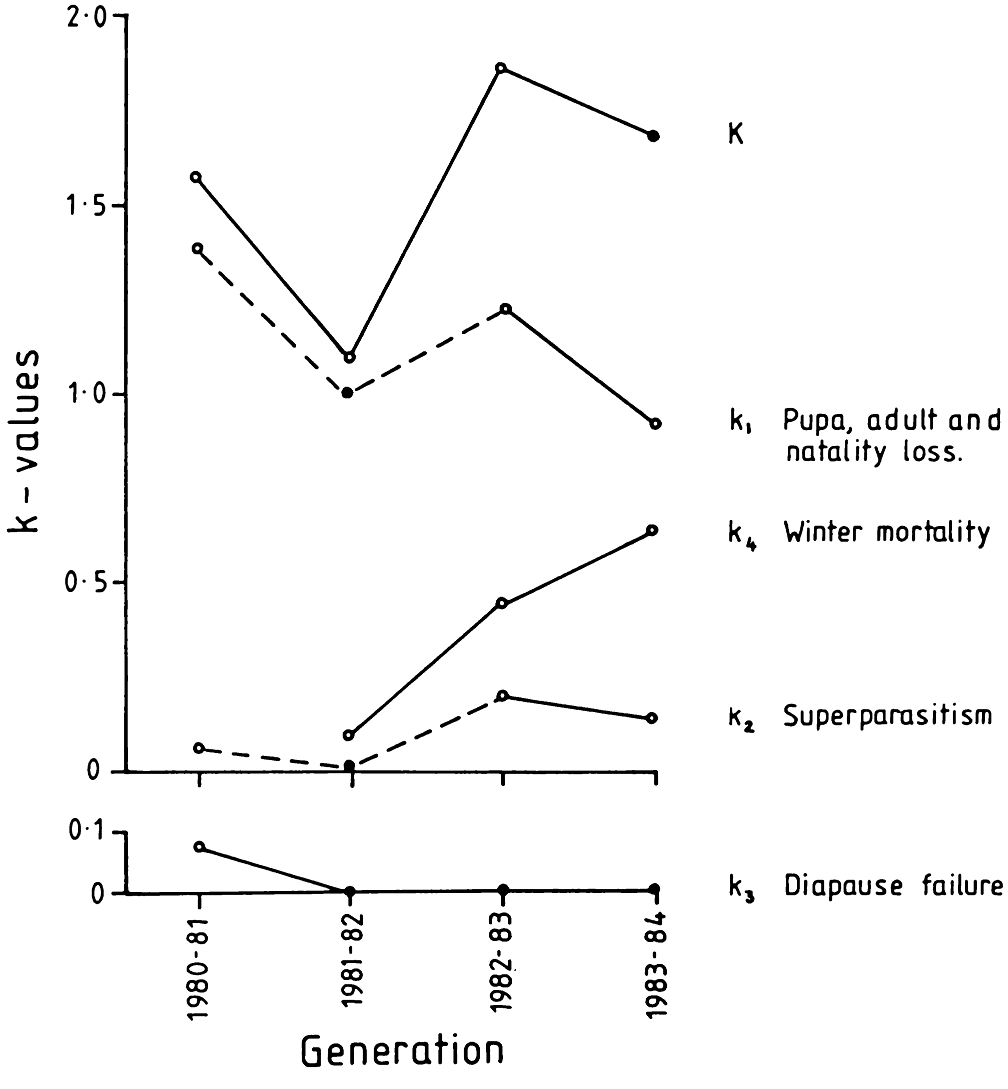


Fig 14:3 K values for *C. scolypopae* population at Steele's Farm, 1981-84.

0) but the same result occurred when the method of Podoler and Rogers (1975) for key factor identification was tried as an alternative (calculated b values; k_1 0•21, k_2 0•23, k_3 0•01, k_4 0•57 : 1981 ommitted in k_4 test. Appendix 22). The variance covariance matrix indicates that k_4 varies inversely with k_1 and k_3. When plotted against parasite density, an inverse density dependent relationship appears likely (Fig 14:4c), but with the few generations studied, the relationship was not significant (t=4•934 0•2<P<0•1) and was not improved when individual block values are analysed.

The second most important factor in determining population variance was k_1 (pupal and adult mortality and variation in natality). When site k_1 values were plotted against P_n, the relationship was only significant at near 10% (t=2•9) but when block values were used, the linear relationship was very significant (t=3•572 P<•01)(Fig 14:4a). Density dependence was not proved without doubt as only one of the proof b values differed significantly from 1 (b_{xy}=•19+•53, b_{yx}=•41±1•2). It is of note that k_1 in Fig 14:4a appears to have a curved rather than linear relationship with increasing density (curve fitted by eye) which may indicate a functional response by the ovipositing females.

Superparasitism (k_2) and diapause failure (k_3) were the least important k factors. From the variance covariance matrix, k_2 appears to be independent of k_1 and showed no density dependent action when plotted against number of female eggs laid (oviposition holes)(Fig 14:4b). As diapause failure (k_3) only occurred once under the known influence of hot summer conditions, it has no obvious density dependent action and was not tested for such.

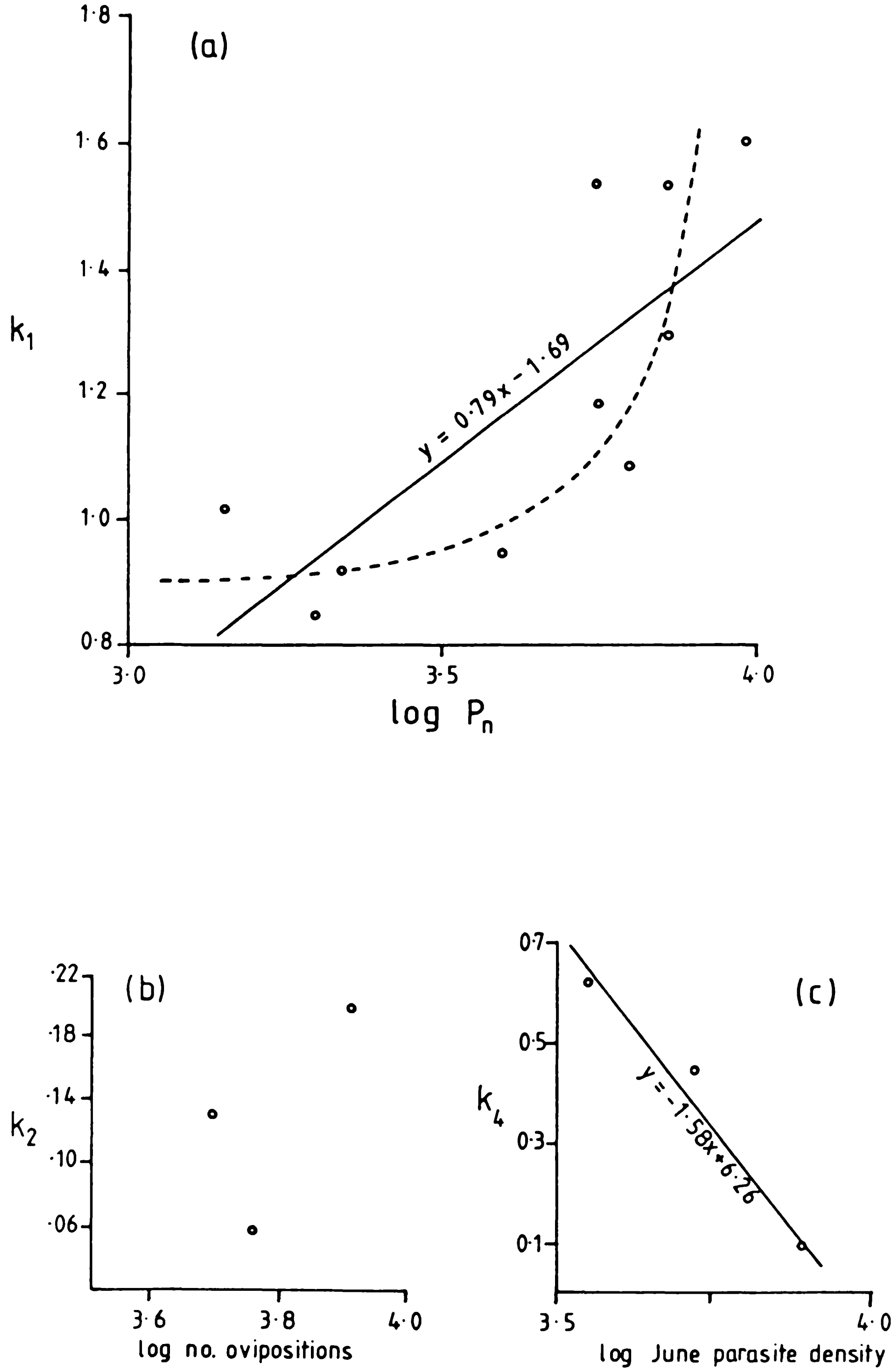


Fig 14:4 Relationship of k factors to log of numbers entering the stage.

2. Parasite efficiency

The basic parameter commonly used to evaluate parasite searching efficiency is its area of discovery, a, (Nicholson 1933, Nicholson and Bailey 1935). This was calculated for each block each year using the equation

$$a = (1/P_n) \times \log_e(N/N_s)$$

where P_n = density of searching parasites

N = density of available hosts

N_s = density of hosts surviving parasitism

This model is based on the assumption that 'a' was constant and that the parasite was mainly limited by its searching ability. Although the assumptions are no longer accepted (Beddington 1975), the model is still used as an index of parasite efficiency. Since there is no direct estimate of searching parasites, in this case Pn is the density of *C. scolypopae* larvae after winter the previous year.

The area of discovery of *C. scolypopae* was found to be related to host density (Fig 14:5a) ($t=2{\cdot}30$ $P<{\cdot}05$). The area of discovery was also related to P_n ($t=3{\cdot}49$ $P<{\cdot}01$)(Fig 14:5b) and it was therefore possible to estimate the Quest constant (Q) and the Mutual interference constant (m) of Hassell and Varley (1969) where

$$\log_{10}a = \log_{10}Q - m\log_{10}P_n$$

This model describes the response of a parasite to its own density when 'a' tends to decrease with increasing density of searching parasites (Hassell and Huffaker 1969). It is known that searching efficiency cannot continue to rise indefinitely as parasite density decreases and that a curvilinear response is more likely such as

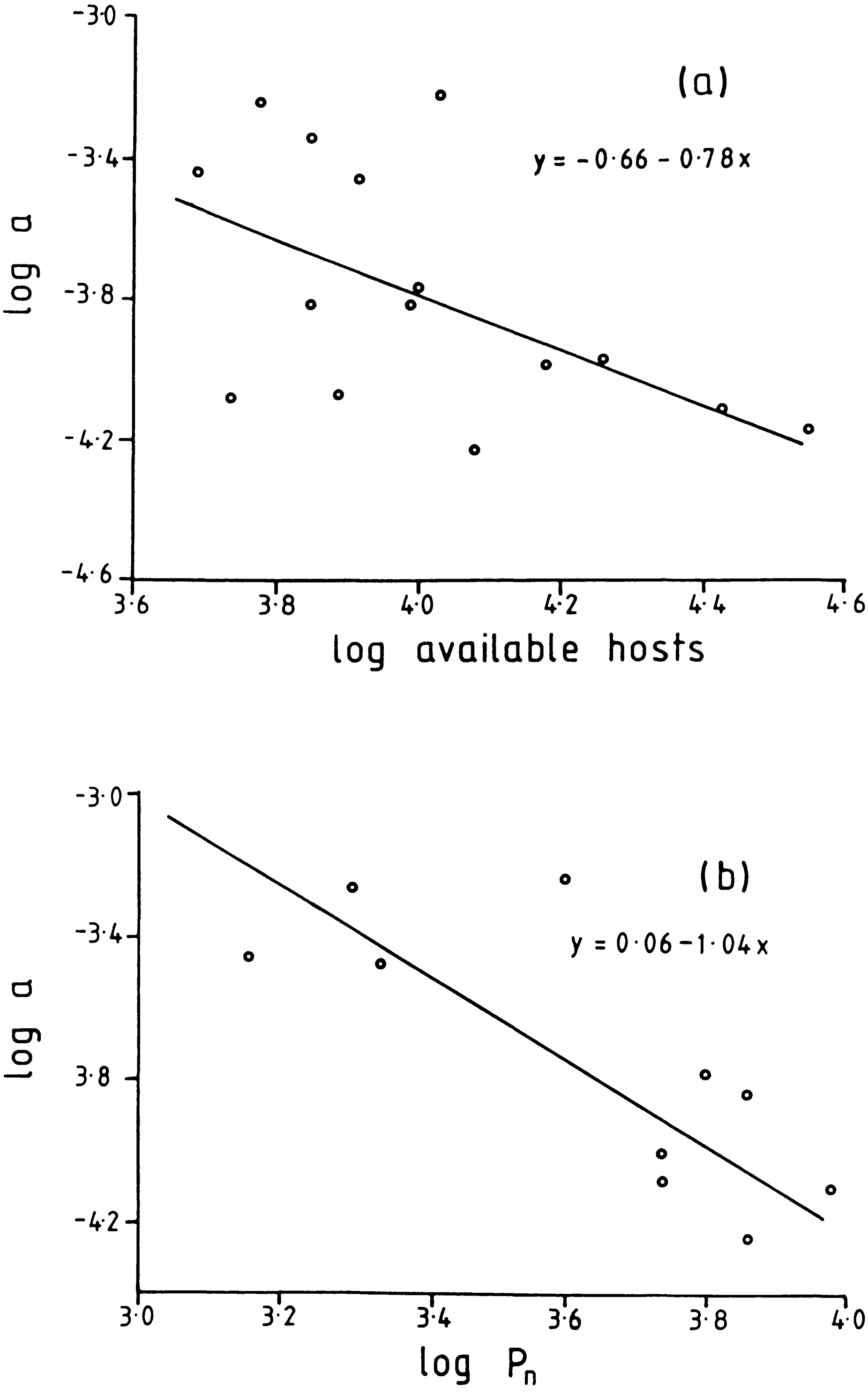


Fig 14:5 Relationship of 'area of discovery' (a) to density of: a, Available hosts and b, parasite density.

predicted by Rogers and Hassell (1974) and Beddington (1975). However, in the absence of reliable information about *C. scolypopae* handling time and longevity, the above model gives adequate description of the limited data available.

For *C. scolypopae*, m=1•04 and Q=•055. Since both the axes included Pn, the significance of the relationship was tested by the method of Hassell and Varley (1969). The log of the k value for parasitism of each block (Y) was plotted against log P_n (X). The regressions of Y on X and X on Y were calculated but although the slopes of both lay below a slope of unity, only one differed from it significantly (b_{xy}= 0•027±•48, b_{yx}=0•079±1•40), and thus did not confirm the existence of interference.

3, Effect of host density

When the density of parasitised *S. australis* eggs is plotted against total density of *S. australis* eggs, a close relationship can be seen (Fig 14:6a) (t=5•244 P<•05) indicating that female parasite numbers (= parasitised eggs) are highly dependent on the number of available hosts. The relationship appears to represent a Type 1 function response (Holling 1959) which can be expressed as

$$N_a = a'T_sN$$

where N_a is ith density of parasitised hosts, a′ is the attack coefficient, T_s is the time available for searching and N is the number of available hosts.

However, if the block values are plotted for each generation individually, differences appeared. For example, a curvilinear Type II

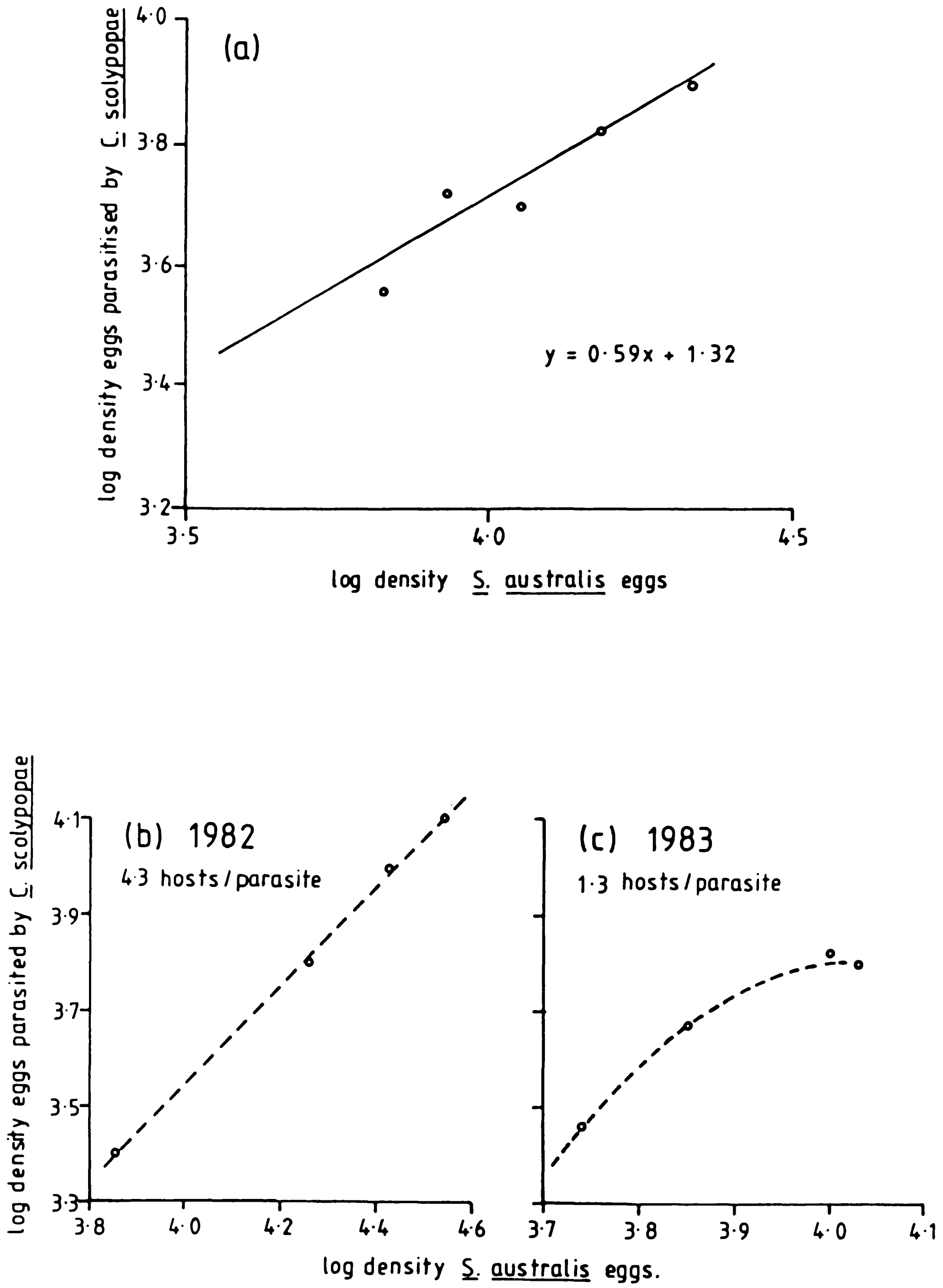


Fig 14:6 Number of *S. australis* parasitised by *C. scolypopae* in relation to host density.: a, Site estimates from each generation.; b, Block estimates from 1982.; c, Block estimates from 1983.

function (Holling 1959) was apparent in 1983 when parasite competition was high (1·32 hosts/P_n) (Fig 14:6c) but in 1982, when competition was less (4·3 hosts/P_n), there was no evidence of any diminishing in the rate of parasite attack (Fig 14:6b). (Dotted lines fitted by eye).

The Type II response, with the number of attacks decreasing to an upper plateau, is widespread amongst insect parasites (Hassell 1976) and is represented by Holling's (1959) equation

$$N_a = a'NT/1+a'T_hN$$

where T is time available for parasitism and T_h the handling time. If there is a significant linear relationship between proportion of host surviving and host density, T_h and a' can be calculated and used to predict N_a as done by Dransfield (1979). However, no significant relationship was found using block data from a single year.

The changing proportions of available hosts each generation, and the associated effects of parasite competition, could be incorporated into this model in the expressions a' and T_h. However there is a further factor that affects the number of hosts parasitised in the *C. scolypopae* - *S. australis* interaction and this is the effect of the the host plant on *S. australis* susceptibility.

A moderate but changing proportion of the *S. australis* egg population is laid in blackberry where it is less vulnerable to parasitism because of greater egg depth. Such spatial asynchrony was incorporated into population models by Hassell and May (1973,1974) in the expression

$$N_{t+1} = FN_t\sum(\alpha_i \exp(-a\beta_i P_t))$$
$$P_{t+1} = cN_t(1-\sum\alpha_i \exp(-a\beta_i P_t)) \quad \text{(Model 1)}$$

where α_i and β_i are the fraction of hosts and parasites respectively in the ith of n patches. In the interaction studied, the two plant species would correspond to two 'patches'. The fit of the Hassell and

May model (Model 1) to the observed parasite densities was tested using the pameters in Table 14:4. For comparison, the Nicholson and Bailey (1935) model, which has no allowance for spatial asynchrony, was also tested. It is represented by the expression

$$P_{t+1} = cN_t\left(1-\exp(-aP_t)\right) \quad \text{(Model 2)}$$

The calculations of the models were started with the observed number of mature larvae (P_n) in October 1980. The 'area of discovery' used was a constant, based on the means of parasitism suffered by the whole population each generation, in order to equalize the overall searching efficiency of the parasites in the two models.

From Fig 14:7, it can be seen that Model 1 fits the observed data closely whereas model 2 overestimates parasite numbers in years of low available hosts (1983 and 1984). The incorporation of the blackberry refuge into the basic model (Model 1) decreases parasite population in every generation but by having the greatest effect in years of low available hosts, it contributes to the stability of the host-parasite interaction by allowing a greater proportion of the hosts to evade parasitism.

When the number of the surviving host eggs occuring in blackberry is expressed as a % of total survivors in the population and is plotted against total eggs laid (Fig 14:8), it can be seen that the % appears to increase as population density decreases. With only 5 generations and the variation in the proportion of total eggs laid in blackberry, the relationship was not significant ($t=1{\cdot}738$ $0{\cdot}2<P<0{\cdot}1$). If the proportion did change inversely with population density, it would provide a powerful stabilising mechanism to the population interaction.

Fig 14:7 Observed parasite population density/m², Oct. 1981-84, and predicted density using Model 1 (incorporating spatial asynchrony) and Model 2.(no asynchrony).

I standard error

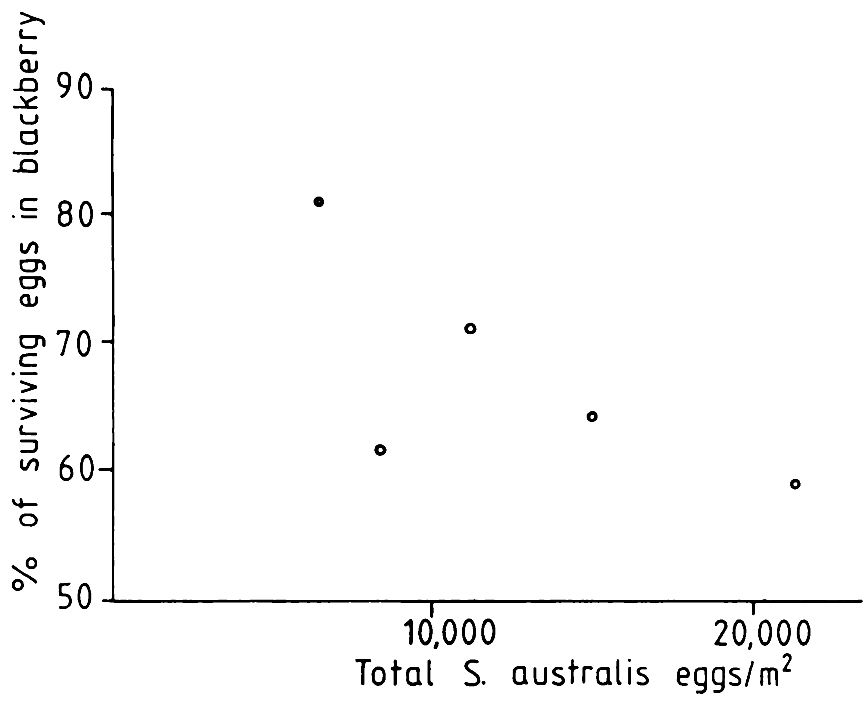


Fig 14:8 Relationship between % survivors in population of *S. australis* eggs occuring in blackberry and population density.

Table 14:4 Parameters used in Model 1 and Model 2 of the *C. scolypopae* population.

Parameter	Value	Derivation
Area of discovery (a)	$1{\cdot}15\text{x}10^{-4}/\text{m}^2$	observed mean 1981-84
Females surviving per host attacked (c)	$0{\cdot}47$	mean Nov/June density 1982-84
Average proportion host in blackberry (α_1)	$0{\cdot}45$	observed mean 1980-81
Average proportion parasite in blackberry (β_1)	$0{\cdot}32$	observed mean 1980-81
Average proportion of host in blackberry (α_2)	$0{\cdot}55$	observed mean 1980-81
Average proportion parasite in bracken (β_2)	$0{\cdot}68$	observed mean 1980-81
Host density (N)	Census data (Table 9:2)	

IV DISCUSSION

Key factor analysis of the life tables of *C. scolypopae* revealed that the key factor responsible for variation in population density from generation to generation was winter mortality (k_4). This was unexpected as mortality factors acting on parasite stages were not thought to contribute significantly to parasite population dynamics by Benson (1973). In his study on *Bracon hebetor* (Hymenoptera : Braconidae), he found that variation in fecundity of female parasites, which reflects searching efficiency, was the key factor.

The lack of any statistical significance to the apparent inverse density dependent relationship between k_4 and June parasite numbers in fig 14:4c , even when individual blocks are tested, is evidence that no real relationship exists. It is difficult to see how the main causes of mortality (fungal attack, stem loss and tunneling insects) could act in an inverse density dependent manner over winter. However it is possible that the incidence of fungi decreases when there are a high number of available hosts per parasite female and thus less chance of susceptible parasitised, and especially superparasitised, eggs being adjacent to each other even when there are high numbers of parasites/m^2. It is reasonable that k_4 could vary inversely with k_1 as indicated in Table 14:3 as then the incidence of fungi, to which *C. scolypopae* is susceptible, could act in a density dependent manner.

The second most important k factor was k_1. The combination of pupal and adult mortality with variation in natality in k_1 may have masked the latter's relationship with total K. However, field observations suggest pupal mortality to be minimal and the high numerical value of k_1 is mostly the contribution of variation in natality. There was no significant density dependence between k_1 and the number of searching adults (P_n) nor with host density. Nor does there seem to be any direct relationship with climatic conditions during the study period although the highest value did occur in the hot 1981 summer and the next in the cold 1983 summer.

Much of the variation in natality may reflect parasite searching efficiency. The significant relationship found between the area of discovery and P_n, according to the model, indicates increasing interference between parasites as density increases. The interference constant (m) is an important contributor to stability of models of host-parasite interactions (Hassell and Varley 1969, Hassell and May 1973, Podoler 1974). For *C. scolypopae* m is close to 1, a value representing a high level of interference and which Hassell and May (1973) have predicted theoretically to be at the upper limit of stability for all values of host rate of increase. Most estimated values for other insect parasites lie in the range 0•2-0•7 (Hassell 1971) but a similar m value was found by Cameron and Redfern (1978) with *Torymus nigritarsus* (Hymenoptera : Torymidae). With both this and *C. scolypopae*, a proportion of the host population has a refuge. With *C. scolypopae*, the eggs laid in blackberry are not as available as those in bracken, and with *T. nigritarsus*, not all galls are equally susceptible. Such an instance when a portion of the host population is protected from parasitism, is given the term spatial asynchrony. The possibility of spatial asynchrony has not been allowed for in the Nicholson and Bailey (1935) and Hassell and Varley (1969) models and thus the use of m as a measure of degree of interference between searching parasites may be misleading. The ease of oviposition in bracken hosts, compared to blackberry, could lead to aggregation and more frequent encounters with other adults and already parasitised eggs. Indeed, if blackberry parasites are excluded from calculations, m rises to 1•26 ($t=3•86$ $P<•01$) which Hassell and May (1973) predict gives rise to unstability in all cases.

Spatial and temporal asynchrony, along with aggregation, give heterogeneity in the distribution of the parasite. Such heterogeneity has been incorporated into population models (Hassell and May 1973, 1974, May 1978, Murdoch and Oaten 1975, Hassell and Anderson 1984). The conclusions have been that in general it raises the equilibrium population levels and enhances stability. This stabilising action was found by Griffiths (1969) in a study of two ichneumon parasites where there was difficulty in locating European pine sawfly pupae at any depth in pine needle litter. The partial refuge of *S. australis* in blackberry, especially if the % of the host protected increases as *S. australis* populations decrease, increases the stability of its interaction with *C. scolypopae* as indicated by the rise in the value of m when blackberry is excluded. Heterogeneity can act at the lowest population levels and is considered one of the main reasons for the persistence of host-parasite interactions leading to successful biological control (Beddington, Free and Lawton 1978).

A further factor that would affect the value of m is superparasitism. Rogers and Hassell (1974) introduced the effect of superparasitism into models and noted that when it occurred, the relationship between log a and log Pn was affected by both the time wasted and host density. Increasing either increased the slope of the relationship, m.

The Quest constant has no effect on stability but can markedly affect the equilibrium levels of the parasite and prey populations. The Quest constant of •055 indicates a low equilibrium density compared with those that would be associated with *Muscidifurax raptor* (0•465; Podoler and Mendel 1979) and *Torymus* (1•514; Cameron and Redfern

1978).

Superparasitism and the remaining k factor, diapause failure, were of little importance to the overall population dynamics of *C. scolypopae*. Superparasitism mortality (k_2) was inversely related to the number of available host eggs per parasite and as expected, it peaked in 1983, when host egg numbers dropped substantially with the cool summer, but numbers of parasite searching remain unaffected.

Many publications on host-parasite relationships are based on laboratory populations and may overemphasize factors such as searching efficiency in overall population regulation. The 96% survivorship of *Mucidifurux raptor* (Hymenoptera:Pteromalidae) (Podoler and Mendel 1979), the low combined mortality of eggs, larvae and pupae found in *Bracon hebetor* (Benson 1973) and the lack of a relationship between mortality of *Nemeritis canescens* and host density (Hassell and Huffaker 1969) could all change in field circumstances. The finding of winter mortality as the key factor determining the fluctuations in the *C. scolypopae* population serves to exemplify the importance of studies of natural populations.

Many publications are concerned with searching ability but mortalities that may affect field populations are only mentioned in passing. This study of the population dynamics of *S. australis* has only opened the door to the complex processes that regulate its numbers and influence its interaction with *S. australis*. Any attempt to produce a complete predictive model is beyond the scope of this study, but it has provided an insight into the multitude of components in the host-parasite relationship, each of which could be the basis for further intensive investigation.

SUMMARY

Although several unsuccessful attempts have been made to introduce exotic natural enemies to control *S. australis* populations, little attention has been given to the ecology of this insect or its interaction with the existing parasite, *C. scolypopae*. This study on the population ecology of both *S. australis* and *C. scolypopae* provides basic information on the factors that influence the population dynamics of both insects and how they interact with each other. The main findings of the study were;

1, A modification of Scott's (1965) height frequency method for vegetation sampling was found to be a very practical method for sampling *S. australis* egg batches in bracken and blackberry. Not only did it provide an absolute estimate of egg batch density, but also the distribution of eggs between host plants and within the canopy, as well as the frequency and distribution of host plants. The method was relatively nondestructive and quick.

2, *S. australis* eggs are predominantly laid in dead twigs in the sheltered middle zone of the vegetation. Peak numbers of eggs were laid in 1980 (~75,000/m^2) and 1982 (~105,000 m^2) and lowest numbers in 1983 (0,000/m^2) and 1984 (~30,000/m^2). Blackberry is preferred to bracken as an oviposition material, even though less abundant.

3, Parasitism by *C. scolypopae* was the largest egg mortality factor. Host plant had a strong influence on parasitism. Bracken had higher levels than blackberry. Fungal infection was the second largest factor and showed increased incidence after winter. Parasitised eggs were susceptible to fungi but as it was not possible to distinguish the primary cause of mortality in most of these cases. Some egg mortality already caused by parasitism would thus be included in the fungal mortality. Destruction of eggs by stem boring insects was the third major cause of mortality with destruction greatest after winter and in blackberry. Increasing height of eggs within vegetation had a positive influence on egg survival, particularly in blackberry. Parasitism was less in the upper canopy, compared to the rest of the vegetation, while the incidence of fungi increased markedly towards ground level. The only mortality factor to increase with vegetation height was destruction of eggs by stem boring insects.

4, Even though *S. australis* eggs are laid over several months, there is considerable synchronisation of hatching in spring, with some eggs taking as little as 189 days to develop and others over 245 days.

5, *S. australis* eggs were incubated at various constant temperatures. The lower temperature threshold for egg eclosion was 10°C, although embryo development reached completion at this temperature. Eggs collected from the field before egg swelling had occurred, just prior to blastokinesis, failed to hatch when held at high humidity at 20 and 25°C but did at 13 and 15°C. The thermal requirement for the completion of the egg stage was about 530 day degrees.

6, The rate of *S. australis* nymphal development was found to differ markedly from year to year. The slowest development was in the cold summer of 1982-83 and the fastest in 1984-85. When development was plotted against cumulative day degrees from egg hatch, instead of days, the difference between years disappeared, showing the strong influence of temperature and the possibility of using day degrees to predict population development.

7, *S. australis* was reared from newly emerged nymphs to adults at 15, 20 and 25°C. Linear regression equations were calculated for each temperature to predict the thermal requirement for a population to reach maturity. The combined laboratory egg and nymphal estimates indicated that 1500-1900 day degrees were required for *S. australis* to complete its life cycle. This requirement is probably responsible for the restriction of *S. australis* to the warmer areas of New Zealand.

8, The development of nymphs on blackberry was behind that of those on bracken. Crozier stage bracken had higher nitrogen content than vegetative blackberry but levels decreased as pinnae unfurled. Blackberry was the main host plant in spring but as the season progressed, most of the population switched to bracken. It was considered that this was due to changes in the physical attributes of the plants. In spring, most blackberry shoots are thick and succulent, but as flowering buds are produced, the stems become thin and lignified and the *S. australis* nymphs move to the more hospitable bracken. No preferential relationship with N content was evident.

9, The *S. australis* nymphal populations follow the same pattern as egg numbers with high numbers from 1980-82 falling to very low numbers in 1983-84 and a small increase in 1984-85. The sharp decline in *S. australis* population density was considered to have been caused by the cold temperatures during the 1982-83 summer which delayed the appearance of adults and shortening the oviposition period. The reduced number of eggs laid were then heavily parasitised by *C. scolypopae* females, the density of which was determined by the previous *S. australis* generation and thus little affected by the cold conditions.

10, Time specific life tables were constructed to determine the relative importance of mortalities acting on the *S. australis* population. Parasitism by *C. scolypopae* was found to be the key factor and had a delayed density dependent action. The next most important factors were variation in natality and adult loss. Neonate loss was the largest mortality and nymphal mortality the smallest. No direct density dependent mortalities were found.

11, Many aspects of the biology and morphology of *C. scolypopae* were described for the first time. The three instars all showed a reduced morphological differentiation compared to other aphelinid species, apparently an adaption to the existence as an egg parasite. The first instar lacked visible segmentation, mouthparts or trachea and retained the remains of the egg chorion like a cap. The second instar had small transparent triangular mouthparts. The final instar had clear segmentation with a distinct cephalic skeleton and chitinised tapering mouthparts. Instead of the usual nine open spiracles found in most chalcidoidea, only four pairs were found. The prepupal stage of the third instar could be easily distinguished by the appearance of a dark bar in the lower third of the host egg chorion. The reproductive systems of both sexes were described. The female internal genitalia were similar to those of other aphelinids, apart from the acid gland which was made up of loosely linked large cell masses around a central duct, rather than the usual tubular gland. The external ovipositor mechanism was longer than most aphelinids and the long ramus had 7 spines instead of the common 6. These differences are adaptions to the depth of the embedded hosts. The male internal genitalia differed markedly from other hymenoptera but the external genitalia were similar to that of some aphelinids.

12, The study of *C. scolypopae* mating behaviour showed that males used their forelegs to vigorously flick the antennae of the females during courtship. This behaviour has not been observed in the Aphelinidae previously.

13, *C. scolypopae* adult longevity was only one day when starved, but increased markedly when honey or *S. australis* honeydew was provided. The lack of nectar sources in the study site during *C. scolypopae* adult activity makes it likely that honeydew is the main nutrient source for adults.

14, *S. australis* egg depth was found to vary with plant species. Those in bracken were laid at shallower depths than those in blackberry. The average length of the *C. scolypopae* ovipositor was 0•6mm. Many eggs in blackberry were found to be beyond the reach of the parasite, and this explained the low parasitism levels observed. In barberry, eggs laid at shallow depths in the thorns had high parasitism levels, whilst those laid in the softer stems had low parasitism. When percentage parasitism for each host plant was plotted against mean egg depth in that plant, a significant linear relationship was found.

15, *C. scolypopae* superparasitism was found to occur, although when parasite oviposition scar distribution was compared to a random (Poisson) distribution, it was apparent that *C. scolypopae* females could discriminate between parasitised and nonparasitised eggs. The progeny of the first oviposition were dominant and eliminated the younger individuals by physiological suppression.

16, *C. scolypopae* is an arrhenotokous species. In bracken, the sex ratio was 1:0•6 in favour of the females. This appeared to be flexible and varied with the plant species and level of superparasitism. Male numbers increased with increasing superparasitism.

17, The lower temperature threshold for *C. scolypopae* varies with the developmental stage. Egg eclosion requires at least 10°C while around 14•5°C is needed for initiation of pupation and adult emergence.

18, *C. scolypopae* has a facultative diapause. At 15°C, all parasites enter diapause during the barred prepupal stage, irrespective of photoperiod. At 20°C, all parasites reared in darkness entered diapause, but none when reared in a long photoperiod. At 25°C, no diapause occurred in the dark. Evidence of two generations of *C. scolypopae* per year was found in two areas in Northland in 1982. In the study site there was only one generation per year in most years, well synchronised with the oviposition period of *S. australis*. However, in 1981, temperatures were high during the months of *C. scolypopae* oviposition and larval development, and many of the parasites failed to enter diapause. Highest of the blocks was Block AT, with 60% of parasites pupating and 35% emerging during winter. No evidence was found that the these adults oviposited successfully.

19, *C. scolypopae* were collected from the field at intervals and exposed to long photoperiods or held in darkness at 20 and 25°C.

Those collected up till early June were found not to have entered diapause and it appeared that diapause was completed by the start of November. Subsequent development of *C. scolypopae* was considered to be highly dependent on temperature, with the margin between the lower threshold for parasite pupation and emergence and that for *S. australis* development, synchronising the appearance of *C. scolypopae* adults and host eggs.

20, A partial analysis was made of the population dynamics of *C. scolypopae*. It was found that mortality of overwintering larvae was the key factor determining the fluctuations of the *C. scolypopae* population. This was independent of density. The second most important factor was the combination of pupal and adult mortality and variation of natality. Density dependence was indicated but not proved conclusively. There appeared to be a curvilinear relationship between this mortality and P_n, indicating a possible functional response by searching females.

21, The 'area of discovery' of *C. scolypopae* was related to both host density and P_n. The mutual interference constant (m) was very close to 1 indicating a high level of interference, theoretically close to the upper limit of stability in host-parasite interactions.

22, *C. scolypopae* numbers were highly dependent on the number of available host eggs. When there were low numbers of hosts per parasite, a curvilinear Holling Type II relationship was apparent but when number of available hosts per parasite was high, there was no evidence of any diminishment of attack rate.

23, *S. australis* eggs were less vulnerable to *C. scolypopae* in blackberry than in bracken. The observed data was found to closely fit the Hassell and May (1974) population model incorporating spatial asynchrony, whereas a similar model without spatial asynchrony overestimated parasite numbers when host population numbers were low. The partial refuge of *S. australis* in blackberry increases the stability of the host-parasite interaction as indicated by the rise in the value of m when blackberry data is excluded from the estimates.

Appendix 1. Mean number of egg batches per m^2 and mean egg batch size for each block at Steele's Farm, Rukuhia, 1980-81.

		Mean no. egg batches/m^2		Mean egg batch size	
Date	Block	Bracken	Blackberry	Bracken	Blackberry
Oct 1980	AT	1104±153	408±66	6•65±0•13	7•51±0•24
	AB	1368±235	768±238		
	BT	823±221	1360±173	6•21±0•18	8•94±•26
	BB	2340±239	330±156		
Area mean		1371±108	754±85		
June 1981	AT	531±128	474±80	7•35±0•73	8•25±1•06
	AB	1200±164	930±311	6•05±0•73	8•65±0•98
	BT	360±50	1205±217	6•45±0•68	8•10±0•95
	BB	1053±165	427±104	6•10±0•59	7•95±1•00
Area mean		757±64	784±101		
June 1982	AT	392±92	440±262	6•72±0•76	10•14±0•93
	AB	3328±938	528±188	8•80±0•49	11•06±0•52
	BT	832±347	1120±100	8•54±0•90	9•54±0•93
	BB	1968±405	1192±250	7•70±0•69	9•24±0•37
Area mean		1567±257	835±101		
Nov 1982	AT	ns	ns	ns	ns
	AB	2096±438	328±212	8•86±0•60	11•24±1•67
	BT	568±192	512±88	9•26±0•46	9•20±0•64
	BB	1544±182	584±220	8•78±0•78	8•90±0•38
Area mean		1333±163	478±97		

Appendix 1 continued

June 1983	AT	768±283	244±130	7·12±0·69	8·22±0·15
	AB	520±229	104±94	8·44±0·62	9·20±0·55
	BT	720±167	550±255	7·72±0·45	10·16±0·32
	BB	864±353	336±117	7·50±0·45	9·14±0·35
Area mean		719±129	323±88		
Nov 1983	AT	ns	ns	ns	
	AB	320±174	90±40	8·38±0·58	9·70±0·77
	BT	200±91	300±89	7·68±0·43	8·52±0·66
	BB	330±117	60±29	7·48±0·30	8·17±0·62
Area mean		276±73	163±38		
June 1984	AT	ns	ns	ns	
	AB	464±245	216±84	8·38±0·53	9·84±0·34
	BT	328±165	512±102	9·16±0·69	10·54±0·40
	BB	224±33	224±60	9·14±0·21	11·06±0·31
Area mean		338±99	334±51		
Oct 1984	AT	ns	ns	ns	
	AB	200±107	40±25	6·96±0·35	10·24±0·94
	BT	88±23	120±46	8·16±0·44	10·04±0·33
	BB	112±23	16±16	8·60±1·35	11·34±1·10
Area mean		130±35	64±20		

Appendix 2. Density of total and surviving *S. australis* eggs.

Date	Block	Total eggs	Surviving eggs
Oct 1980	Site A	12600±1320	3200±440
	Site B	17400±1840	5400±680
	Area total	15120±1160	4320±400
JUNE 1981	AT	7820±1460	3480±720
	AB	15300±3140	7160±1760
	BT	12080±2140	5920±1640
	BB	9820±1500	2142±600
	Area total	11280±1080	4740±680
JUNE 1982	AT	7099±2750	3117±2088
	AB	34987±9196	11463±3851
	BT	18054±3510	7839±1723
	BB	27017±5268	9777±2971
	Area total	21399±2745	7984±1335
Oct 1982	AT	ns	ns
	AB	20602±3438	3757±1139
	BT	10242±1542	3570±699
	BB	18552±2055	4748±1022
	Area total	15947±1363	3987±541

Appendix 2 continued

JUNE 1983	AT	7081±1195	1187±316
	AB	5443±2103	698±319
	BT	10665±3093	2286±1012
	BB	9979±2764	1478±547
Area total		8429±1250	1465±341
Oct 1983	AT	ns	ns
	AB	3739±1371	418±169
	BT	4251±799	864±326
	BB	2918±922	408±213
Area total		3687±593	588±152
JUNE 1984	AT	ns	ns
	AB	6058±2377	1278±465
	BT	8304±1580	2590±672
	BB	4650±1108	1981±539
Area total		6501±1010	2004±340
Oct 1984	AT	ns	ns
	AB	1934±1068	422±257
	BT	1906±527	678±269
	BB	1270±439	310±127
Area total		1721±408	488±136

APPENDIX 3. Percentage survival of *S. australis* eggs in each block at Steele's Farm, Rukuhia 1980, 1982, 1983 and 1984.

DATE	BLOCK			
	AT	AB	BT	BB
BRACKEN				
Oct 1980	16±1		19±3	
June 1982	16•6±2•4	25•0±6•8	24•5±7•8	11•9±2•4
Nov 1982	14•8±3•5	13•7±3•6	30•0±7•4	22•9±4•8
June 1983	14•7±3•0	9•3±3•8	9•2±4•6	4.8±2•3
Nov 1983	ns	11•6±4•2	11•3±5•6	9•8±3•5
June 1984	ns	10•6±1•9	10•6±4•3	15•5±1•7
Oct 1984	ns	11•8±3•6	10•9±2•3	22•0±3•1
BLACKBERRY				
Oct 1980	42±2		44±3	
June 1982	45•2±7•2	53•0±6•2	52•9±4•9	64•5±8•2
Nov 1982	36•1±5•1	47•5±9•3	39•8±9•1	39•7±5•8
June 1983	34•4±4•4	40•8±9•6	32•2±3•4	32•2±8•5
Nov 1983	ns	22•7±6•4	22•2±6•7	21•0±3•1
June 1984	ns	39•7±5•2	41•7±8•9	57•8±10•4
Oct 1984	ns	45•0±4•8	44•5±7•0	43•3±10•2

APPENDIX 4. Percentage fungal infected *S. australis* eggs in each block at Steele's Farm, Rukuhia 1980, 1982, 1983 and 1984.

DATE	BLOCK			
	AT	AB	BT	BB
	BRACKEN			
Oct 1980	25±1		22±3	
June 1982	9•6±3•7	15•7±3•0	6•8±1•4	15•5±4•1
Nov 1982	14•9±5•1	22•5±7•9	13•7±1•0	24•9±5•2
June 1983	5•9±1•9	21•7±1•4	18•6±2•2	19•2±1•9
Nov 1983	ns	22•4±4•8	20•8±4•0	31•0±4•7
June 1984	ns	4•4±1•5	2•6±1•3	3•8±1•1
Oct 1984	ns	25•4±7•0	8•3±1•6	12•1±3•9
	BLACKBERRY			
Oct 1980	28±2		18±3	
June 1982	2•2±0•3	7•7±2•5	5•2±1•0	4•2±2•3
Nov 1982	10•0±2•7	18•1±9•5	18•2±12•2	11•6±4•0
June 1983	2•9±2•1	13•0±6•8	2•8±0•4	3•1±1•2
Nov 1983	ns	27•2±10•8	21•2±5•8	13•7±3•8
June 1984	ns	1•8±0•5	1•3±0•8	3•1±1•8
Oct 1984	ns	11•4±4•5	7•4±2•5	5•9±2•1

APPENDIX 5. Percentage overlaid *S. australis* eggs in each block at Steele's Farm, Rukuhia 1980, 1982, 1983 and 1984.

DATE	BLOCK			
	AT	AB	BT	BB
		BRACKEN		
Oct 1980	ns	ns	ns	ns
June 1982	1·0±0·7	1·5±0·8	0·9±0·4	3·9±1·9
Nov 1982	0·5±0·3	1·5±1·1	3·3±1·2	1·5±0·6
June 1983	0·2±0·2	0	2·3±1·4	2·1±1·4
Nov 1983	ns	0·5±0·3	0·3±0·3	0
June 1984	ns	0·7±0·5	0·8±0·8	1·8±1·3
Oct 1984	ns	0·5±0·3	1·1±0·8	0
		BLACKBERRY		
Oct 1980	ns	ns	ns	ns
June 1982	3·6±2·3	6·0±3·6	3·6±1·6	1·6±1·6
Nov 1982	3·5±2·0	2·0±1·1	4·0±2·3	1·2±0·5
June 1983	3·4±1·0	4·0±1·0	2·9±1·2	3·2±2·3
Nov 1983	ns	1·6±1·4	0·4±0·3	3·9±1·4
June 1984	ns	0·8±0·4	4·1±1·7	8·0±3·9
Oct 1984	ns	6·1±3·2	3·2±1·3	1·8±1·1

APPENDIX 6. Percentage *S. australis* eggs destroyed by stem boring larvae in each block at Steele's Farm, Rukuhia 1980, 1982, 1983 and 1984.

DATE	BLOCK			
	AT	AB	BT	BB
		BRACKEN		
Oct 1980	ns	ns	ns	ns
June 1982	0	0	3·7±3·7	0
Nov 1982	0·8±0·8	0	1·6±1·6	7·1±4·4
June 1983	0	0	0	0
Nov 1983	ns	2·2±1·6	0·4±0·4	0·6±0·6
June 1984	ns	0	0	0
Oct 1984	ns	0	0	0·1±0·1
		BLACKBERRY		
Oct 1980	ns	ns	ns	ns
June 1982	4·9±4·9	3·3±2·2	1·5±1·5	0
Nov 1982	7·2±4·4	4·8±4·8	1·0±1·0	14·2±9·9
June 1983	0·5±0·5	0·6±0·4	0·9±0·9	0
Nov 1983	ns	5·8±2·4	3·3±1·8	5·2±3·0
June 1984	ns	1·2±1·2	7·2±4·0	0
Oct 1984	ns	0	3·9±1·7	14·4±6·8

APPENDIX 7. Percentage *S. australis* eggs parasitised by *Centrodora scolypopae* in each block at Steele's Farm, Rukuhia 1980, 1982, 1983 and 1984

DATE	BLOCK			
	AT	AB	BT	BB
		BRACKEN		
Oct 1980	55±2		53±4	
June 1982	58·7±5·6	41·1±1·9	51·8±5·1	59·9±8·8
Nov 1982	60·8±5·5	47·4±10·4	44·2±8·0	37·4±6·1
June 1983	73·4±2·7	61·9±4·9	66·1±4·7	67·4±2·1
Nov 1983	ns	54·2±7·0	59·4±5·5	51·0±7·4
June 1984	ns	78·2±2·2	80·5±3·3	73·0±3·0
Oct 1984	ns	58·6±9·3	77·2±3·0	61·5±5·9
		BLACKBERRY		
Oct 1980	24±2		29±3	
June 1982	33·9±8·0	19·6±4·6	25·1±5·3	19·4±7·4
Nov 1982	31·2±8·5	18·7±3·3	26·7±3·7	21·4±6·2
June 1983	46·4±7·6	38·6±5·8	55·5±3·6	58·5±6·7
Nov 1983	ns	37·3±5·9	49·1±7·8	50·6±3·7
June 1984	ns	48·9±7·9	41·7±9·6	26·9±12·6
Oct 1984	ns	34·3±5·9	33·6±4·6	29·7±7·4

APPENDIX 8. Percentage other mortality factors of *S. australis* eggs in each block at Steele's Farm, Rukuhia 1980, 1982, 1983 and 1984.

DATE	BLOCK			
	AT	AB	BT	BB
		BRACKEN		
Oct 1980	4±1		5±2	
June 1982	14•2±4•6	16•7±3•8	12•2±3•5	9•9±3•3
Nov 1982	8•2±1•2	14•9±7•3	7•3±1•4	6•2±0•7
June 1983	5•8±1•1	7•1±2•4	3•9±0•9	6•5±2•1
Nov 1983	ns	9•2±4•3	7•9±2•4	7•6±0•6
June 1984	ns	6•0±1•3	5•6±1•5	6•0±1•5
Oct 1984	ns	3•7±2•1	2•6±1•0	4•3±1•7
		BLACKBERRY		
Oct 1980	6±1		10±2	
June 1982	10•2±3•9	10•4±2•3	11•8±1•1	10•3±1•8
Nov 1982	12•1±5•5	9•0±1•9	10•3±3•8	12•0±2•9
June 1983	12•4±4•3	3•0±0•8	5•8±1•2	3•0±0•6
Nov 1983	ns	9•2±4•3	7•9±2•4	7•6±0•6
June 1984	ns	7•6±2•0	3•9±1•3	4•2±1•3
Oct 1984	ns	3•2±0•7	7•6±3•0	4•9±1•3

Appendix 9. Effect of vegetation height on the survival of *S. australis* eggs. 1981 (mean % for whole site ± SE).

		May		October	
Block	Height	Bracken	Blackberry	Bracken	Blackberry
AT	High	31±4	68±4	16±3	22±3
	Med	16±4	73±3	1±1	26±3
	Low	24±4	59±3	4±2	2±1
AB	High	27±3	81±3	41±4	47±4
	Med	43±5	50±4	33±4	37±4
	Low	38±4	38±4	7±2	21±3
BT	High	40±5	69±4	25±4	37±4
	Med	42±4	51±4	26±4	42±4
	Low	22±3	43±4	14±3	35±3
BB	High	31±4	50±4	8±2	47±4
	Med	15±3	35±4	16±3	31±4
	Low	15±3	43±4	5±2	32±3

Appendix 10. Effect of vegetation height on the incidence of fungae in *S. australis* eggs. 1981 (mean % for whole site ± SE).

		May		October	
Block	Height	Bracken	Blackberry	Bracken	Blackberry
AT	High	3±2	4±2	6±2	7±2
	Med	3±1	5±2	8±2	4±1
	Low	11±3	2±1	49±5	13±3
AB	High	8±2	3±1	5±2	14±3
	Med	3±2	2±1	11±3	7±2
	Low	7±2	3±1	57±4	8±3
BT	High	4±2	1±1	8±3	0±0
	Med	3±1	8±2	4±2	19±3
	Low	10±3	15±3	21±4	10±2
BB	High	7±2	7±2	11±3	12±2
	Med	10±3	4±2	38±4	29±3
	Low	19±3	19±3	13±3	5±2

Appendix 11. Effect of vegetation height on the parasitism of *S. australis* eggs. 1981 (mean % for whole site ± SE)

		May		October	
Block	Height	Bracken	Blackberry	Bracken	Blackberry
AT	High	56±4	21±3	66±3	43±4
	Med	62±4	13±3	58±4	39±4
	Low	48±5	31±3	46±4	27±3
AB	High	64±4	12±2	36±4	19±3
	Med	47±5	40±4	28±4	31±4
	Low	48±4	43±4	78±4	1±1
BT	High	38±5	28±4	60±5	15±3
	Med	52±4	29±4	63±4	13±3
	Low	58±4	38±4	52±5	37±3
BB	High	56±4	25±4	51±4	14±3
	Med	70±4	59±4	34±4	13±3
	Low	57±4	30±3	72±4	40±3

Appendix 12. Effect of vegetation height on the destruction of *S. australis* eggs by stem boring larvae. 1981 (mean % for whole site ± SE)

		May		October	
Block	Height	Bracken	Blackberry	Bracken	Blackberry
AT	High	0±0	0±0	0±0	18±3
	Med	0±0	2±1	6±2	24±3
	Low	0±0	0±0	0±0	14±3
AB	High	0±0	0±0	1±1	25±3
	Med	0±0	0±0	3±1	4±2
	Low	0±0	0±0	0±0	0±0
BT	High	0±0	0±0	0±0	37±4
	Med	0±0	7±2	0±0	9±2
	Low	0±0	1±1	0±0	0±0
BB	High	0±0	0±0	0±0	5±2
	Med	0±0	0±0	5±2	0±0
	Low	0±0	0±0	0±0	11±2

Appendix 13. 1980-81 *S. australis* nymph and adult population estimates.

		Numbers/stem		Total/m^2	
Date	Block	Bracken	Blackberry	Bracken	Blackberry
6.12.80	AT	2•7±0•3	2•9±0•6		
	AB	4•5±0•7	13•1±2•2		
	BT	21•3±3•2	13•0±3•1		
	BB	16•2±2•8	19•1±2•5		
Site mean		11•7±1•2	12•0±1•2	81•2±13•7*	123±29*
4.1.81	AT	13•0±2•5	4•7±0•7		
	AB	10•2±2•1	4•6±1•0		
	BT	30•5±4•1	12•6±2•2		
	BB	17•6±1•6	8•8±1•5		
Site mean		18•6±1•6	8•0±0•8	133•7±19•1	67±12
19.2.81	AT	35•8±6•3	ns		
	AB	40•4±4•7	ns		
	BT	26•6±3•0	ns		
	BB	ns	ns		
Site mean		34•3±4•1		200•9±27•9*	

ns = not sampled

* = using pooled 1983-84 and 1984-85 stem estimates

Appendix 14. 1981-82 *S. australis* nymph and adult population estimates.

		Numbers/stem		Total/m^2	
Date	Block	Bracken	Blackberry	Bracken	Blackberry
3-19.12.81	AT	18·7±4·3	17·7±4·8		
	AB	17·5±6·8	26·8±4·0		
	BT	10·6±2·4	20·8±4·5		
	BB	8·9±2·0	16·2±5·0		
Area mean		13·8±2·1	20·4±2·1	96±20	137±18*
2-9.1.82	AT	19·8±4·4	6·0±2·2	100±25	24±10
	AB	38·5±12·0	17·4±3·1	326±15	126±18
	BT	45·4±18·2	24·4±3·6	310±139	224±87
	BB	23·8±5·1	18·4±8·3	172±35	109±52
Area mean		32·6±6·3	16·9±2·4	231±55	126±29
21.2.82	AT	33·4±5·8	3·2±2·7		
	AB	37·6±6·0	0·5±0·1		
	BT	21·1±9·4	3·7±1·2		
	BB	7·7±1·5	4·2±0·5		
Area mean		24·8±3·4	3·0±0·8	188±34	16±6*

* = using 1984-85 blackberry stem estimates.

Appendix 15. 1982-83 *S. australis* nymph and adult population estimates.

		Numbers/stem		Total/m^2	
Date	Block	Bracken	Blackberry	Bracken	Blackberry
20.11.82	AT	11•1±2•3	10•0±5•2	60±9	113±90
	AB	12•2±3•1	22•1±4•3	61±18	198±35
	BT	9•3±2•8	10•3±4•8	50±14	53±22
	BB	20•2±10•3	12•3±4•6	117±64	75±26
Area mean		12•9±2•3	13•4±2•4	70•7±16•2	106•1±24•9
7.12.82	AT	20•7±9•4	ns		
	AB	30•9±5•2	ns		
	BT	11•8±1•3	ns		
	BB	24•4±6•2	ns		
Area mean		21•3±3•0	ns	148±21*	
18.12.82	AT	23•4±13•5	ns		
	AB	40•9±11•2	ns		
	BT	23•0±4•3	ns		
	BB	22•8±11•3	ns		
Area mean		27•1±5•1	ns	188±44*	

Appendix 15 continued.

3.1.83	AT	24·4±7·0	ns	
	AB	44·1±7·7	ns	
	BT	38·1±8·3	ns	
	BB	22·2±8·1	ns	
Area mean		32·5±3·9	ns	233±39*
16.1.83	AT	18·2±2·4	ns	
	AB	ns	ns	
	BT	19·0±4·1	ns	
	BB	ns	ns	
Area mean		18·6±2·5	ns	141±25*
30.1.83	AT	17·0±6·4	ns	
	AB	19·6±5·6	ns	
	BT	10·0±2·8	ns	
	BB	12·2±5·0	ns	
Area mean		14·4±2·5	ns	109±22*
13.2.83	AT	8·2±3·7	ns	
	AB	12·9±3·9	ns	
	BT	11·0±4·0	ns	
	BB	19·2±1·9	ns	
Area mean		12·7±1·8	ns	96±18*

Appendix 15 continued

3.3.83	AT	7•2±1•1	ns	
	AB	33•8±9•4	ns	
	BT	20•3±3•6	ns	
	BB	34•6±4•1	ns	
Area mean		23•5±2•6	ns	178±28*
31.3.83	AT	2•3±0•4	ns	
	AB	3•5±1•4	ns	
	BT	2•6±0•8	ns	
	BB	10•1±1•4	ns	
Area mean		4•5±0•5	ns	34±6*

* = estimates using pooled 1983-84 and 1984-85 bracken stem data.

ns = not sampled.

Appendix 16. 1983-84 *S. australis* nymph and adult population estimates.

		Numbers/stem		Total/m^2	
Date	Block	Bracken	Blackberry	Bracken	Blackberry
13.11.83	AT	ns	ns	ns	ns
	AB	3•3±0•9	7•0±2•0	12•9±3•3	91•1±23•7
	BT	0•8±0•5	0•9±0•3	3•3±2•0	18•3±6•6
	BB	1•9±0•6	5•5±1•9	10•6±4•1	71•1±28•1
Area mean		1•9±0•4	4•2±0•9	8•4±1•8	56•7±11•5
1.12.83	AT	ns	ns	ns	ns
	AB	3•8±1•5	6•2±2•1		
	BT	2•5±0•8	3•4±1•0		
	BB	1•1±0•7	0•1±0•1		
Area mean		2•4±0•6	3•3±0•8	15•0±4•9	44•6±14•0*
15.12.83	AT	ns	ns	ns	ns
	AB	7•4±2•6	2•2±0•6	62•3±24•9	26•7±10•6
	BT	4•0±1•7	3•0±1•2	26•8±14•5	33•8±8•5
	BB	2•5±1•8	0•4±0•3	17•6±11•7	7•3±5•6
Area mean		4•6±1•2	2•0±0•5	34•8±10•1	23•5±4•9

Appendix 16 continued

3.1.84	AT	ns	ns	ns	ns
	AB	3•6±0•7	2•1±0•3		
	BT	4•0±0•9	2•2±0•5		
	BB	3•4±2•0	1•2±0•6		
Area mean		3•7±0•7	1•9±0•3	28•1±7•2	23•4±5•3*
17.1.84	AT	ns	ns	ns	ns
	AB	3•2±0•8	1•0±0•4	20•1±4•7	7•3±2•4
	BT	5•6±2•0	1•0±0•4	55•0±22•1	14•9±6•1
	BB	0•8±0•4	1•0±0•4	6•7±3•3	12•6±6•5
Area mean		3•4±0•8	1•0±0•2	29•6±8•8	11•9±3•2
30.1.84	AT	ns	ns	ns	ns
	AB	2•6±0•6	1•1±0•3		
	BT	2•5±1•0	2•0±0•6		
	BB	1•7±0•7	0•4±0•2		
Area mean		2•3±0•5	1•3±0•3	17•3±4•7	10•5±4•3*

Appendix 16 continued.

14.2.84	AT	ns	ns	ns	ns
	AB	4•6±2•2	1•0±0•3	35•6±19•6	3•4±0•6
	BT	5•9±2•3	6•1±2•5	47•6±26•8	28•0±12•3
	BB	1•5±1•0	4•4±1•3	11•4±8•8	25•4±12•0
Area mean		4•1±1•4	4•0±1•1	32•9±12•3	20•1±6•0
13.3.84	AT	ns	ns	ns	ns
	AB	2•8±0•4	0•8±0•3		
	BT	1•2±0•3	3•0±1•5		
	BB	3•0±0•5	3•5±0•9		
Area mean		2•2±0•2	2•5±0•7	16•5±3•1	11•3±4•6**

* = estimated using stems/m^2 from preceding and following sampling dates.

** = estimated using stems/m^2 from preceding sampling date.

Appendix 17. 1984-85 *S. australis* nymph and adult population estimates.

		Numbers/stem		Total/m^2	
Date	Block	Bracken	Blackberry	Bracken	Blackberry
20.11.84	AT	ns	ns	ns	ns
	AB	8·0±3·7	10·3±4·0	28·2±10·6	86·1±46·8
	BT	5·4±1·7	6·0±1·9	25·4±7·8	26·6±9·7
	BB	7·8±2·1	5·5±1·3	23·7±5·1	69·2±20·9
Area mean		6·9±1·5	7·2±1·5	25·7±4·7	57·8±16.1
2.12.84	AT	ns	ns	ns	ns
	AB	6·12±2·4	8·4±4·0	33·1±10·0	56·4±26·7
	BT	5·5±1·8	5·6±1·8	33·6±9·6	30·7±9·2
	BB	11·3±2·3	12·4±2·6	62·4±16·5	89·6±17·6
Area mean		7·5±1·2	8·5±1·6	42·3±7·0	56·6±10·4
16.12.84	AT	ns	ns	ns	ns
	AB	9·3±4·3	8·3±2·6	57·3	45·7*
	BT	4·1±1·0	4·5±1·1	31·4	22·0*
	BB	6·5±0·8	7·2±1·0	36·6	72·9*
Area mean		6·4±1·4	7·2±1·0	40·9	44·8*

Appendix 17 continued.

1.1.85	AT	ns	ns	ns	ns
	AB	8•9±1•0	4•2±1•0	56•5±7•5	19•2±5•4
	BT	5•2±1•8	2•4±0•5	30•8±9•0	8•6±1•9
	BB	10•0±2•7	6•3±1•6	59•4±19•2	45•2±11•3
Area mean		7•8±1•1	4•2±0•6	47•4±7•2	23•0±3.9
30.1.85	AT	ns	ns	ns	ns
	AB	28•0±6•6	8•8±3•0	174•7±31•7	38•6±8•1
	BT	6•0±1•6	1•8±1•0	66•5±35•6	4•6±75•6
	BB	30•2±6•0	9•8±3•1	198•1±44•6	85•5±41•8
Area mean		20•1±2•8	6•4±1•4	139•8±21•7	41•4±13•1
17.2.85	AT	ns	ns	ns	ns
	AB	8•9±2•1	0•6±0•3	59•8±16•7	3•1±1•3**
	BT	5•4±1•0	0•9±0•4	45•4±15•9	4•0±1•8**
	BB	10•8±1•9	3•7±0•9	69•9±14•5	27•9±8•4**
Area mean		8•0±1•9	1•7±0•5	57•3	11•0

* = estimated using stems/m^2 from preceding and following sampling dates.

** = estimated using stems/m^2 from preceding sampling date.

Appendix 18. *S. australis* development (mean instar) at Steele's Farm, Rukuhia 1980-84 . Means for bracken on each block.

Date	AT	AB	BT	BB
1.12.80	2·70±·12	2·45		
8.12.80			2·38	2·31
2-4.1.81	4·90±·01	4·56±·18	4·16±·04	4·19±·03
19.2.81	6·00	6·00	6·00	5·99
3.12.81	1·53±·08	1·80±·06	1·03±·06	1·43±·09
2-4.1.82	4·57±·12		3·78±·05	3·52±·03
9.1.82		4·57±·09		
21.2.82	6·00	6·00	6·00	6·00
20.11.82	1·91±·06	1·34±·11		
25.11.82			1·43±·12	1·25±·04
7.12.82	2·64±·09	2·29±·13	1·93±·02	2·10±·02
18.12.82	3·29±·06	2·94±·11	2·78±·06	2·90±·02
3.1.83	4·20±·09	3·93±·11	3·67±·05	3·63±·05
16.1.83	4·77±·06		4·37±·05	
30.1.83	5·11±·12	5·10±·11	4·82±·05	4·95±·09
13.2.83	5·90±·04	5·66±·09	5·65±·10	5·57±·08
3.3.83	5·99±·01	5·97±·01	5·99±·01	5·98±·01
31.3.83	6·0	6·0	6·0	6·0

Appendix 18 continued

13.11.83	ns	1•60±•24	1•47±•13	1•57±•15
1.12.83	ns	2•21±•19	2•25±•19	1•94±•09
15.12.83	ns	3•52±•14	2•94±•20	2•84±•09
3.1.84	ns	4•47±•19	3•87±•03	3•71±•24
17.1.84	ns	5•18±•15	4•90±•04	4•95±•06
30.1.84	ns	5•70±•14	5•52±•22	5•19±•15
14.2.84	ns	6•00±•00	5•97±•02	5•99±•01

2.11.84	ns	2•12±•21	1•74±•03	1•81±•06
2.12.84	ns	3•14±•15	2•95±•09	2•91±•06
16.12.84	ns	4•01±•17	3•90±•07	3•76±•07
1.1.85	ns	5•12±•16	4•86±•04	4•79±•06
30.1.85	ns	5•99±•01	5•99±•01	6•00±•0

Appendix 19 *S. australis* development (mean instar) at Steele's Farm, Rukuhia 1980-84 . Means for blackberry on each block.

Date	AT	AB	BT	BB
8.12.80	2·90		2·41	
18.12.80		3·08		2·65
2-4.1.81	4·73±·04	4·42±·12	4·06±·06	3·97±·05
16.12.81	2·37±·06	2·26	1·99±·01	2·07±·03
2-4.1.82	4·27±·07		3·67±·06	3·42±·05
9.1.82		4·28±·05		
21.2.82	6·00	6·00	6·00	6·00
20.11.82	1·55±·11	1·23±·14		
25.11.82			1·28±·12	1·17±·05
13.11.83	ns	1·39±·17	1·51±·20	1·24±·11
1.12.83	ns	2·34±·13	2·11±·10	1·67±·10
15.12.83	ns	3·25±·18	2·87±·10	2·28±·17
3.1.84	ns	4·12±·15	3·80±·02	3·91±·06
17.1.84	ns	4·68±·19	4·8±·10	4·67±·18
30.1.84	ns	5·53±·17	5·22±·04	4·92±·08
14.2.84	ns	6·00±·00	5·93±·03	5·97±·03
2.11.84	ns	2·05±·26	1·65±·10	1·80±·05
2.12.84	ns	3·24±·16	2·73±·05	2·86±·04
16.12.84	ns	3·94±·19	3·85±·05	3·75±·10
1.1.85	ns	4·91±·15	4·79±·05	4·81±·08
30.1.85	ns	5·98±·01	5·98±·03	5·99±·01

Appendix 20 Egg content of females collected at study site 14.2.81-29.4.81.

Date	Site A	Site B
14.2.81	9•78±1•39	
19.2.81	13•72±1•64	16•48±2•06
27.2.81	12•87±0•76	
4.3.81	12•16±1•25	
6.3.81	12•12±1•29	17•35±1•12
10.3.81	16•96±2•18	15•27±2•09
25.3.81	15•00±2•12	
2.4.81	18•50±2•23	
8.4.81	10•43±2•24	
16.4.81	10•29±2•90	
29.4.81	11•50±3•10	

Appendix 21 Density of parasitised *S. australis* eggs 1980-84; block and total area estimates.

		Density
Oct 1980	Site A	5580±600
	Site B	7260±960
	Total	6480±580
June 1981	AT	2940±720
	AB	6680±1780
	BT	4040±1060
	BB	6540±1120
	Total	4960±600
June 1982	AT	2539±531
	AB	12723±3037
	BT	6352±1276
	BB	10332±1090
	Total	7826±846
Oct 1982	AT	ns
	AB	9456±2622
	BT	4021±960
	BB	6306±1452
	Total	6380±989

Appendix 21 continued

June 1983	AT	4854+1175
	AB	2912±1119
	BT	6312±1589
	BB	6563±1640
	Total	5230±715
Oct 1983	AT	ns
	AB	1976±994
	BT	2192±553
	BB	1439±394
	Total	1896±391
June 1984	AT	ns
	AB	4112±1637
	BT	4450±1518
	BB	1997±459
	Total	3597±786
Oct 1984	AT	ns
	AB	1058±614
	BT	878±188
	BB	623±148
	Total	855±207

Appendix 22 Podoler and Roger's test for key factor 1981-1984.

	K	k_1	k_2	k_3	k_4
1981	1·568	1·391	0·060	0·117	
1982	1·089	0·995	0·014	0·000	0·089
1983	1·861	1·223	0·197	0·000	0·441
1984	1·680	0·920	0·136	0·000	0·624
Total	6·198	4·529	0·407	0·117	1·154
mean	1·550	1·132	0·102	0·029	0·385
ss	0·326	0·139	0·020	0·010	0·148
$\sum Kk_i$		7·086	0·704	0·183	1·966*
$\sum K \sum k_i$		7·018	0·631	0·181	1·781*
b		0·209	0·227	0·006	0·562*

* estimated omitting 1981 K

Appendix 23 Estimation of No. *C. scolypopae* eggs laid/m^2

	oviposition holes/egg		No. female eggs		
year/block	br	bl	br	bl	total
1981					
AT	1•18±•04	1•00*	2853±809	522	3375
AB	1•23±•05	1•05*	4207±1243	3423	7630
BT	1•22±•08	1•04*	1471±379	2947	4418
BB	1•25±•05	1•06*	5663±1180	2131	7794
1983					
AT	1•56±•06	1•33*	6043±2335	1302	7347
AB	1•71±•12	1•45*	4432±1935	464	4896
BT	1•61±•13	1•37*	5608±1038	3876	9484
BB	1•75±•11	1•49*	8059±3484	2917	10976
1984					
AB	1•47±•04	1•33±•08	4535±2427	1366±724	5901±2533
BT	1•37±•04	1•17±•05	3206±1564	2469±609	5675±1678
BB	1•54±•05	1•31*	2344±430	622	2966

* 85% of bracken estimate.

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