THE KAROO CATERPILLAR *LOXOSTEGE FRUSTALIS* ZELLER (LEPIDOPTERA: PYRALIDAE) IN RELATION TO ITS HOST PLANTS AND NATURAL ENEMIES

BY

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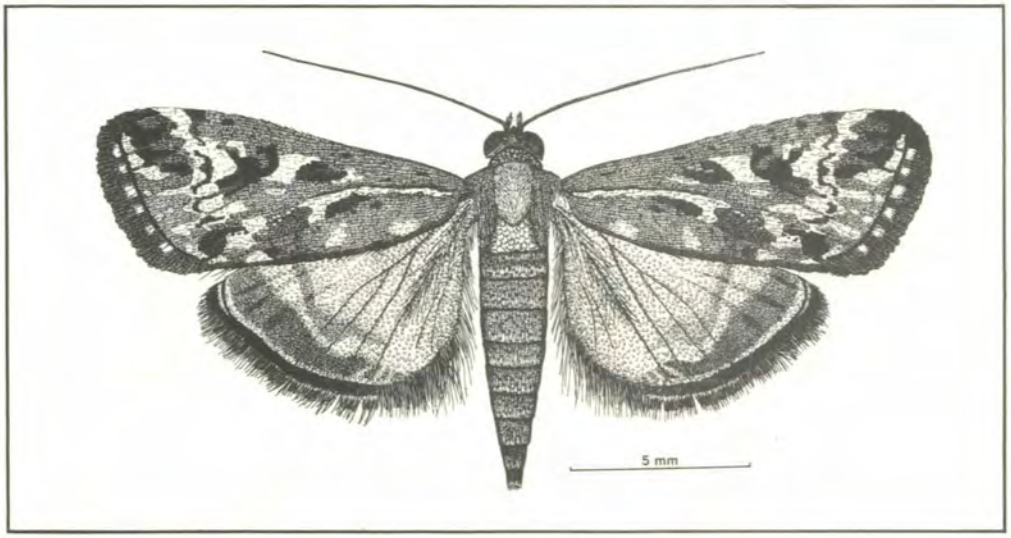
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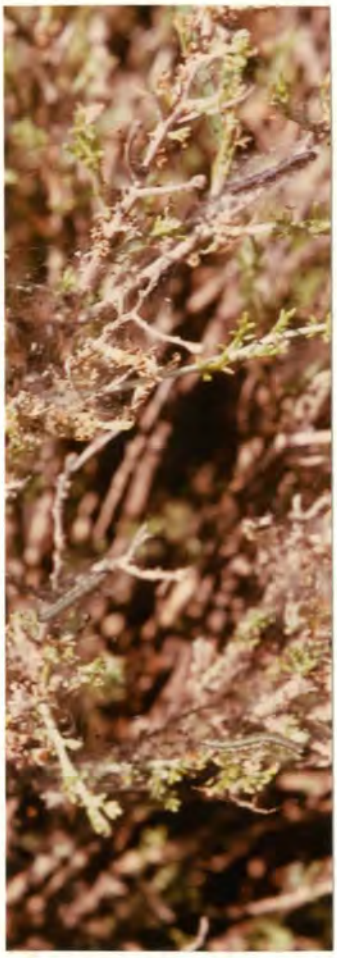

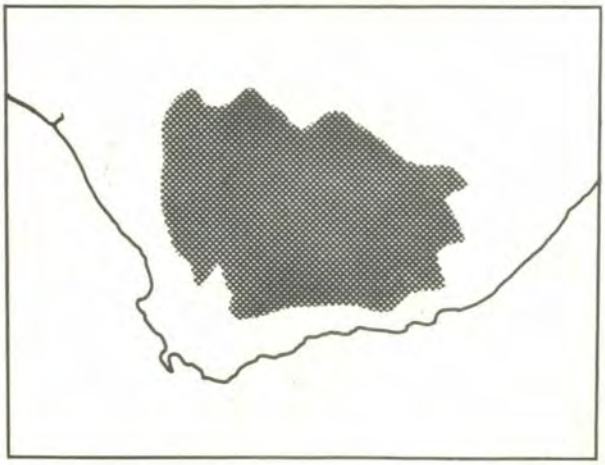

CONTENTS

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1. RÉSUMÉ

The Karoo is an arid inland plateau in the central and northeastern Cape Province of South Africa and is characterised by sparse, stunted vegetation. The vegetation is rich in species, and over large areas species of *Pentzia*, which are drought-resistant shrubs, are extremely abundant. These plants are food for stock (mainly sheep), and because the larvae of the Karoo caterpillar periodically occur in sufficient numbers to defoliate the plants, they assume pest status.

Fully-fed *Loxostege frustalis* larvae construct cases in the soil beneath their food plants and they overwinter in these cases. A census of the numbers of larval cases accumulated in the soil, conducted from 1975 to 1980, showed that an expanded distribution of the pentzias is responsible for the periodic larval outbreaks. Further, alternate food plants are an important food supply for *L. frustalis* larvae when they disperse under crowded conditions

The census data for *L. frustalis* were analysed by constructing partial life tables for the life-history period from case construction to moth emergence. The mortality of 'encased larvae' is useful for assessing the impact of the known *L. frustalis* natural enemies. The most important natural enemies were the braconids *Chelonus curvimaculatus* Cameron, *Macrocentrus maraisi* Nixon and the fungus *Beauveria bassiana* (Balsamo) Vuillemin. The collective responses of all the natural enemies to the density of *L. frustalis* encased larvae was direct, but undercompensating, so that areas with more pentzias produced more *L. frustalis*.

Strategies for immediate measures to alleviate the Karoo caterpillar problem, and for future research, are discussed. It

is concluded that reduction of pentzia populations to acceptable levels and/or supplementing pastures with non-host plants of *L. frustalis* offer the only practical solutions to the Karoo caterpillar problem. Biological control of *L. frustalis* is dismissed as an option for reducing the pest status of the Karoo caterpillar.

2. INTRODUCTION

This study of the Karoo caterpillar *Loxostege frustalis* Zeller centres around a census of larval cases dug from the soil. The data are arranged as partial life tables to examine the roles of host plants and natural enemies as determinants of Karoo caterpillar abundance. This is also a means for a much-needed study on the general biology of the moth and its natural enemies.

Geologically the Karoo is part of the Great Karoo Basin which was shaped by ancient glacial and volcanic activity (Anderson & McLachlan 1976; Cluver 1978; Du Toit 1954; McLachlan & Anderson 1977). Subsequent erosion and change from swampy to arid conditions resulted in the interspersed flat and broken country of the central and northeastern Cape Province now colloquially (and in this thesis) called the Karoo (frontispiece). This region, together with the surrounding areas, considered sensitive to Karoo encroachment, occupies about half of South Africa (Anonymous 1980).

The vernacular word 'Karoo' is derived from the succintly descriptive Hottentot word 'Karrô' which means 'dry place' (G.S. Nienaber 1963; P.J. Nienaber 1963). Climatically (Table 1) the Karoo may be defined, according to the Holridge system (Price 1975), as semi-arid to arid and warm-temperate to cool-temperate. A feature of the climate is a long-term pattern of seasonality in both temperature and rainfall. Rainfall, however, is erratic and often patchily distributed, while unseasonal cold weather is common.

Table 1. Long-term meteorological data for Middelburg in the Karoo (data provided by the Soils and Irrigation Research Institute, Middelburg).

Annual rainfall (mm). Mean ± standard error:	361,0 ± 15,0
Relative humidity range (%). Mean daily minimum and maximum	23,0 - 80,0
Temperature range (°C)	- 12,6 - 41,4
Temperature range (°C). Mean daily minimum and maximum	- 0,5 - 30,3
Temperature range (°C) 5 cm below soil surface	- 1,4 - 45,1
Frost-free period. Range (days)	62,0 - 191,0

Over the past 150 years or so the Karoo fauna and flora have changed significantly. Instead of free-roaming herds of game there are now domesticated animals (mainly sheep) and the pristine vegetation has been largely replaced by karroid veld (Acocks 1975, 1979; Klintworth 1948; Roux 1980, 1981; Tidmarsh 1948). There is general agreement that the process of deterioration is continuing, with desertification advancing northwestwards. Farming is extensive; the recommended stocking rate (Anonymous 1974) varies from about one hectare per small-stock unit in the east to about five in the drier west.

The vegetation, which is rich in species, comprises several Veld Types with strong affinities to the southern fynbos (macchia) and northern savannah (Acocks 1975). Many of the plant communities sampled during this study (frontispiece) physiognomically resemble Biome 18 of Whittaker (1975: Plate 24). In Southwood's (1977a) terminology the Karoo habitat is 'unpredictable', with patches of 'temporary' pioneer vegetation.

Three species of *Pentzia* (Asteraceae) - namely *P. globosa*,

P. incana and *P. spinescens* - are extremely abundant over large areas of the modified Karoo, especially the flats. These species are sympatric, but the sympatry is imperfect and in many districts some of the species are scarce or even absent. In this study, emphasis is placed on the most abundant of the pentzias in each of the census sites. These plants are food for stock and are also the most important food plants of the Karoo caterpillar.

The general biology of *L. frustalis* is discussed in Section 4 and is mainly about the features which are relevant to the census, so that many obviously important aspects of biology are omitted or glossed over - diapause is a good example - but shortcomings in the knowledge about *L. frustalis* are indicated.

L. frustalis is an autochthonous pyraustine which is restricted to southern Africa, with its distribution centred in the Karoo where it periodically occurs in epidemic numbers. The larvae are fully fed in 2 - 3 weeks and then construct cases in the soil beneath host plants. Development of these 'encased larvae' may be more or less arrested ('dormant') before 'emergent' adults escape from the 'spent' cases.

L. frustalis encased larvae may be killed in the cases, usually before pupation, by one of a complex of native natural enemies whose biologies are explained in Section 5. Here too, emphasis is placed on features which relate to the interpretation of the census data, particularly the host relationships. The commonest are *Macrocentrus maraisi* Nixon, *Chelonus curvimaculatus* Cameron (both braconids) and the fungus *Beauveria bassiana* (Balsamo) Vuillemin. Less common are the braconid *Cremnops frustalis* Nixon, the ichneumonid *Temelucha picta* Holmgren and several tachinids. The latter are treated collectively; they were scarce

during the study period and keys to identify them are not yet available.

The most abundant hyperparasitoid is the perilampid *Perilampus rostratus* Kerrich. Rarer hyperparasitoids are the ichneumonid *Stictopisthus breviscapus* Kerrich and chalcidids. Of the latter only *Peltochalcidia capensis* Steffan has been positively identified. Mature chalcidid larvae encountered are all indistinguishable from *P. capensis* and it is probably the only representative of the family. Pending further studies, immature chalcidids were treated collectively.

The bombyliids *Geron* sp., *Exhyalanthrax flammiger* (Walker), *Exhyalanthrax lugens* (Loew) and *Spogostylum incisurale* (Macquart) are all hyperparasitic and generally polyphagous, with a tendency to facultative primary parasitism. *Geron* sp. was not identified to species. J. Bowden (*in litt.* 1979) identified *Geron turneri* Hesse reared from *L. frustalis* but states it may be synonymous with *Geron nomadicus* Hesse.

For the census (Section 6) larval cases were collected in the soil from beneath host plants in various parts of the Karoo from 1975 to 1980. The contents of the larval cases were interpreted in terms of partial life tables for the life-history period between case construction and moth emergence. Two sets of data are provided: the numbers of *L. frustalis* larval cases accumulated in the soil and the numbers of larvae killed, or about to be killed, by various mortality factors. The study does not lead to a key-factor analysis; the data permit only an evaluation of density relationships in space over a relatively small part of the life cycle.

In Section 7 the census data are viewed in the light of differences between plant communities. This pursues the intimation by Greathead (1971) that 'owing to ecological changes on the Karoo ... the Karoo caterpillar became a serious pest', and the hypothesis (Annecke & Moran 1977) that the 'expanded distribution of the Karoo bushes ... and - perhaps more important - an increased density of these species ... (caused) insects that feed on Karoo bushes (to) have gradually assumed increasing importance to man and his animals'. The intuitive suggestion of a positive density-dependent relationship between the abundance of *L. frustalis* and its host plants is substantiated.

The mortality data presented in Section 7 extends the earlier work of Marais (1955). It is a response to the directive of Annecke & Moran (1977) when they wrote that 'In retrospect, it is clear that pre-introduction studies on *L. frustalis* and its parasitoid complex were completely inadequate even for a preliminary hit or miss attempt at biological control ... The lesson is obvious, but even now, in the late 1970's, our knowledge of *L. frustalis* population dynamics and key mortality factors remains scanty'.

An overall strategy for *L. frustalis* control and research priorities is proposed in Section 8. To evaluate natural pastures (veld) is the province of pasture scientists, but perspective on the merits of some plants is essential in the Karoo caterpillar context. The successional status and value to stock farmers of the most abundant pentzias - and therefore the pest status of the Karoo caterpillar - constitute a controversial but vital issue which is discussed at the end of this thesis.

3. GENERAL MATERIALS AND METHODS

LABORATORY CONDITIONS AND REARING

Laboratories were held under a 14 : 10 h light-dark cycle, 25 ± 5°C and 10 - 40% relative humidity. Perspex mating/oviposition cages (25 x 25 x 30 cm) sealed with waxed paper, in which the relative humidity was raised to about 80% with moistened cotton wool, were used. Moths of *L. frustalis* were fed sugar- and honey-solutions. Almost any substrate was found to be suitable for oviposition; the choice of material (paper, organdie, plants, etc.) depended upon requirements. Rearing of *L. frustalis* larvae was on bouquets of host-plants held in florist's foam* or water (basically the method of Marais (1955)) or on an artificial diet (Appendix 1). Larvae were allowed to construct cases in sterilised sand. Pupae were removed from cases before adult eclosion. General handling techniques and sanitation were similar to those recorded by Smith (1966) for rearing phytophagous insects.

Developmental studies were conducted in the laboratory. Measurements were taken using a dissecting microscope fitted with an eye-piece micrometer. Head capsules were measured across their widest part when viewed in silhouette from above; usually head width was measured immediately behind the ocelli. Protruding ocelli were ignored. Clypei were measured across their anterior extremities, also at the widest part. The number of larval instars was determined from the widths of head capsules and clypei arranged into frequency distributions (Atkinson 1980;

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* 'Oasis', manufactured by Elro J. Braak, Pretoria.

Broodryk 1970; Granett 1979). The results were verified by following the development of individuals in captivity. Material for the first three instars was obtained mainly from laboratory cultures; it included both sexes and some were parasitised by *Ch. curvimaculatus*. The last two instars were collected from the field. Live hosts, larval exuviae and remains left by parasitoids were recorded and counted.

To examine the effects of *Ch. curvimaculatus* on *L. frustalis* larval development, adult parasitoids were collected from the field, reared from *L. frustalis* and from a culture maintained on the potato tuber moth *Phthorimaea operculella* (Zeller) according to the method of Broodryk (1969). *L. frustalis* eggs laid during one night were exposed to mated and virgin females of the parasitoid. Daily records of moulting were kept. Host larvae were considered fully fed at the onset of case construction. Rearing was on bouquets of host plants, the first two instars in groups of ten or less in waxed paper cups and singly in perspex Petri dishes thereafter. Parasitism was determined by dissection after the third larval instar or by allowing the parasitoids to develop further.

Adult insects and pathogens were identified by specialist taxonomists. Material was preserved dry or in 70% ethyl alcohol. Small structures were lightly boiled in 5% KOH and mounted in glycerine. Drawings were made with the aid of microscopes fitted with gridded eye-pieces or drawing attachments.

LIGHT-TRAP RECORDS

Nightly catches of *L. frustalis* adults have been recorded

since 1964, at Middelburg (Table 2). Trap catches were manually sorted to collect the *L. frustalis* adults; very big catches were visually quartered prior to sorting. Moths were counted directly, when necessary after sub-sampling by mass. Nightly catches for each month were computed from monthly totals and the number of nights a trap operated. The Wolmarans trap resembled the Pennsylvania type described by Frost (1957). All the data are converted to 'Robinson' values (see Appendix 2). *M. maraisi* adults captured in the light-traps were counted directly.

Table 2. Light traps for studies on *L. frustalis* adults. The Meteorological Station is that of the Soils and Irrigation Research Institute, Middelburg.

Period (July - June annually)	Method	Trap site (Distance (km) from Meteorological Station)
1964 - 1974	Wolmarans (1968)	0
1972 - 1974	Robinson & Robinson (1950)	1,3
1974 - 1980	Robinson & Robinson (1950)	0,5

BOTANICAL ASPECTS

The acceptability of plants as food for *L. frustalis* larvae was evaluated in captivity and in the field. In laboratory feeding trials, separate bouquets of various plants in florist's foam were offered to groups (generally of about 10) of third or fourth-instar larvae in Petri dishes. *P. globosa* was always included as a standard and trials were terminated when these plants were defoliated (fig. 1). Feeding on the other plants was then evaluated on a scale of 5 categories (1 = no feeding; 2 = 1 - 25% defoliation; 3 = 26 - 50% defoliation; 4 = 51 - 75%

defoliation; 5 = > 75% defoliation).

5 cm

Fig. 1. *P. globosa* twigs undamaged and defoliated by *L. frustalis* larvae.

Damage and feeding levels in the field were categorised along similar lines by comparison with the amount of feeding on the dominant pentzias, except only four categories were considered since zero feeding was included in the first quarter. On these bases the host status of plants were rated according to their susceptibility to feeding by *L. frustalis*. Their status was recorded as negligible (little feeding by *L. frustalis* larvae), low, intermediate and high (favoured as a food-plant by *L. frustalis* larvae).

To estimate plant densities in the field, the distance method of Keuls *et al.* (1963) was used to calculate the average distance, from a census sample (see Section 6) to the four

nearest plants of the same species. Chi-squared tests indicated the necessity for square-root transformations to normalise these density estimates. For density counts, plants with more than half their canopies inside quadrats were included. Fifty percent of the plants bisected by the edges of quadrats were discounted. Abundance classes for plant counts were widely used and are described in Appendix 3.

More specific methods used in this study are described in context.

4. THE BIOLOGY OF *L. FRUSTALIS*

This section provides background information on the biological features of *L. frustalis* which are important for the collection and analysis of the census data.

LIFE HISTORY (FIG. 2)

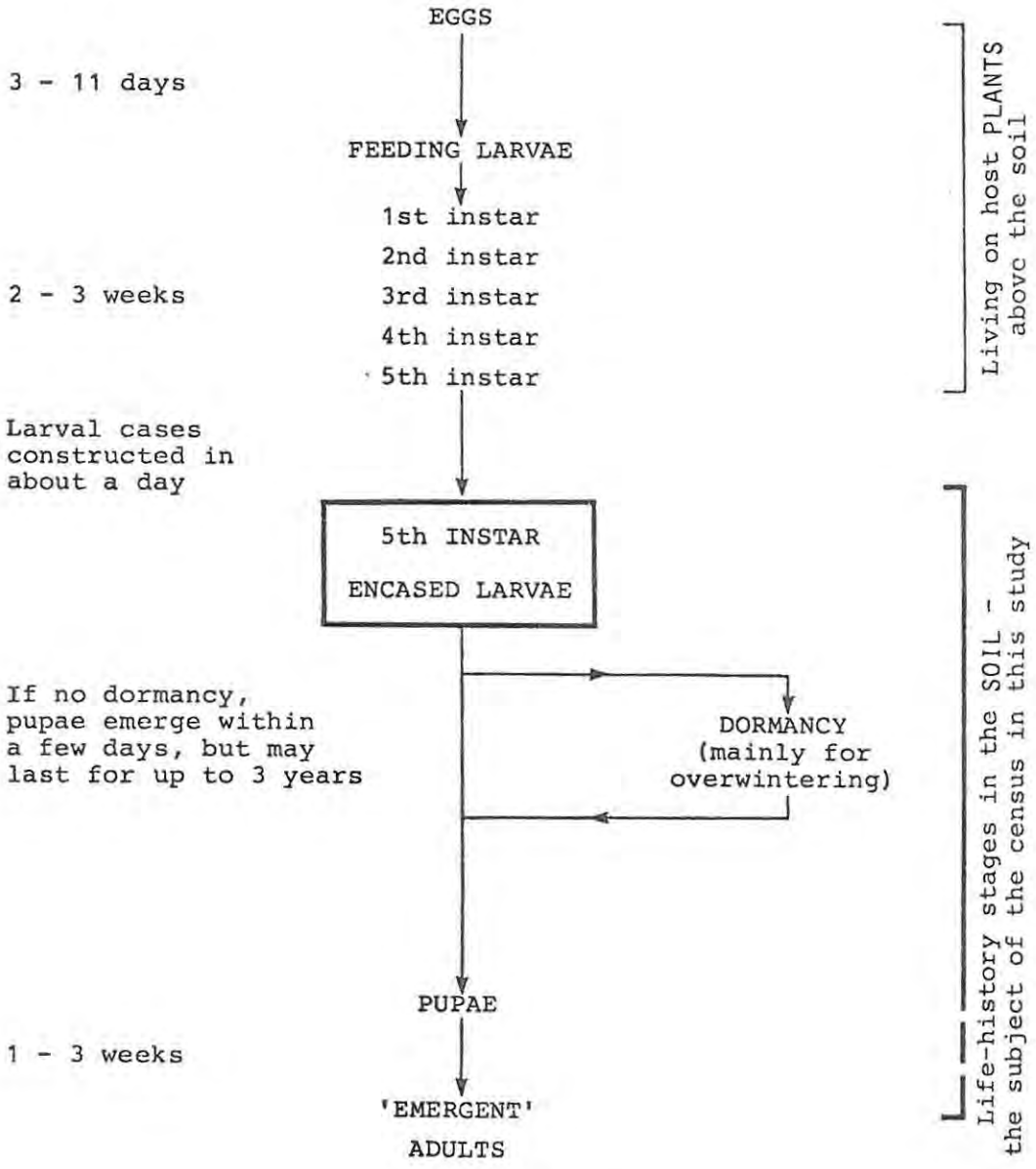

Fig. 2. Salient features of the life history of *L. frustalis*.

Eggs are laid directly on host plants. The larvae pass through five larval instars (see below) and when fully fed they construct cases in the soil beneath host plants. The larvae may undergo a period of facultative dormancy in their cases followed by pupation and adult emergence. Because dormant larvae removed from their cases are active they cannot be strictly regarded as being in diapause (Annecke & Moran 1977). Therefore, the term 'dormant larvae' is used here for what is assumed to be a degree of diapause as reviewed by Masaki (1980). The durations of the stages are shown in Table 3. The minimum generation time is about six weeks, but dormancy in encased larvae may prolong the life cycle for up to several years. The life cycle of *L. frustalis* is similar to that of *Loxostege sticticalis* (L.) (Camprag 1976; Pepper & Hastings 1941; Popov 1976a).

Table 3. The duration of *L. frustalis* stages. Data for this study were obtained under laboratory conditions; pupae were reared from field-collected dormant larvae. *n* = number of observations.

Stage	Duration (days) Marais (1955) and Taylor (1940)	This study (Means ± standard errors)	*n*
Eggs	2,5 - 11 (average 5 - 6)	3	37
Feeding larvae	15 - 24	17,6 ± 0,17[1]	35
Egg and first instar	-	6,8 ± 0,10	45
second instar	-	2,2 ± 0,60	45
third instar	-	2,3 ± 0,07	45
fourth instar	-	2,5 ± 0,08	45
fifth instar	-	4,2 ± 0,11[2]	35
Dormant larvae	up to 3 years	-	
Pupae	7 - 23 (average 15,25)	13,6 ± 0,13	87
males	-	13,4 ± 0,17[3]	51
females	-	13,9 ± 0,21[3]	36
Adults	up to 1 month (average 2 weeks)	-	

[1] Non-cumulative total.

[2] Includes non-feeding period of about 1 day prior to case construction.

[3] Differences between males and females non-significant ($0,1 > P > 0,05$).

MOTH ABUNDANCE

Lounsbury (1897) wrote 'The (Karoo) caterpillars, it is said, appear soon after rains during the summer, and their coming is preceded by immense swarms of moths'. Since then there have been many references to moth numbers, using a variety of superlatives. These are not exaggerations. During six weeks in February - March 1972 8,6 million moths were caught in four light traps, covering 4 ha, at Middelburg, (unpublished data on file, Plant Protection Research Institute, Middelburg). A catch from one trap is illustrated by Annecke & Moran (1977: fig. 2)*.

The moths were most abundant in autumn, and in broad terms the numbers are clearly influenced by climate (figs 3 and 4; Appendix 2). But these data are of limited predictive value - regression analysis would be presumptuous - and the data mainly corroborate earlier observations and suggestions linking moth flights with rainfall (Annecke & Moran 1977; Lounsbury 1897, 1899; Marais 1949, 1955; Taylor 1940, 1962; van Ark 1964; Wolmarans 1968).

The lack of significant correlation between rainfall and moth numbers for some seasons and in the long term (fig. 4) is important. Rainfall is undoubtedly critical but is not the only variable which influences moth numbers. Other short-term effects - weather as defined by Henson (1968) - are important and may override rainfall. For example, Wolmarans (1968) could not show a relationship between rainfall and moth numbers between

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* Through me, the trap was erroneously called a Rothamsted type (Williams 1948), but has since been recognised as a modified Pennsylvania type as described by Frost (1957).

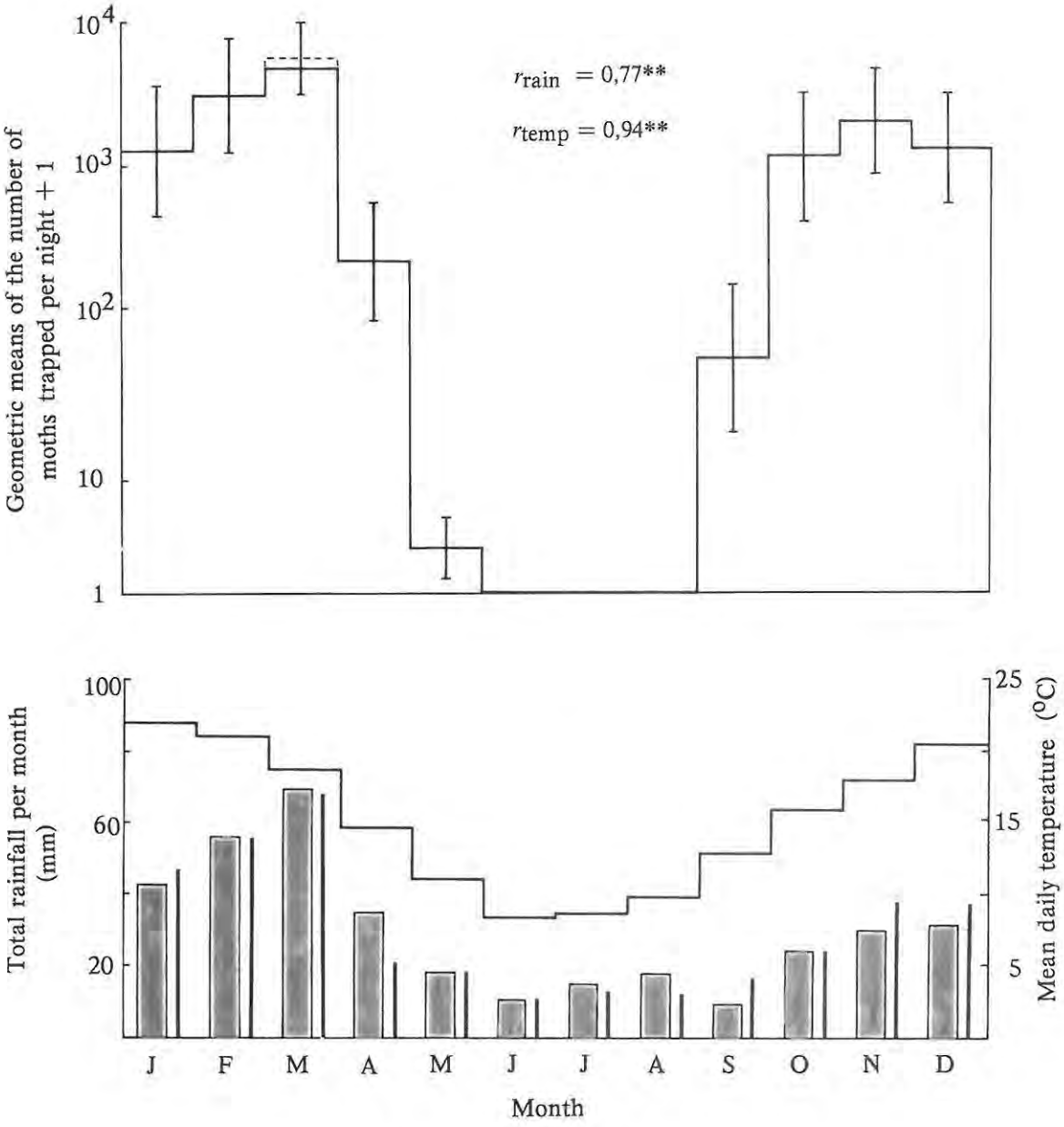


Fig. 3. Light-trap catches of *L. frustalis* adults (top: geometric means of the numbers of moths trapped per night + 1 for each month ± 95% confidence limits), rainfall (bottom, shaded histogram bars) and temperature (bottom, histogram) at Middelburg for the period July 1964 - June 1980. Lines between shaded histogram bars (bottom) show average rainfall from 1916 to 1979. The broken histogram for March (top graph) is explained in Appendix 2. Correlation coefficients (r) are for rainfall/moth catch and for temperature/moth catch for the period 1964 - 1980. Significance of r at $P < 0,01$ (**).

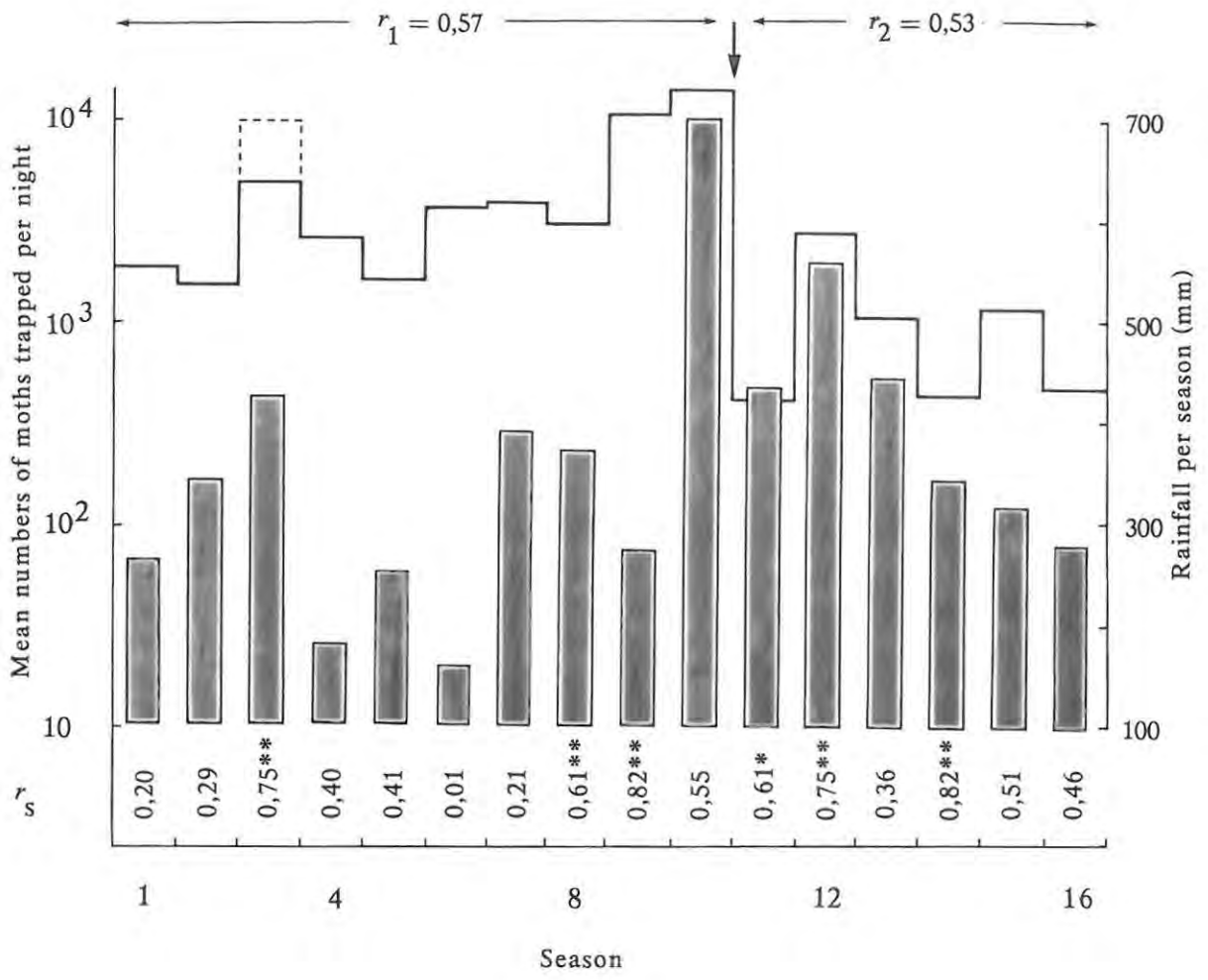


Fig. 4. Light-trap catches of *L. frustalis* adults (histogram) and total rainfall (shaded histogram bars) for consecutive seasons (each from July to June) from 1964 to 1980 at Middelburg. The broken histogram (Season 3) and change in trapping procedure (arrowed) are explained in Appendix 2. Correlation coefficients (r) are for seasonal moth catches and rainfall (r_1 up to Season 10, r_2 from Season 11). Rank correlations (r_s) above the horizontal axis are between monthly moth catches and rainfall within seasons, with adjusted values for March 1967. Significance of r and r_s at $P < 0,05$ (*) and $P < 0,01$ (**).

peak flight periods. Also, moths are often abundant in the Middelburg light traps during prolonged droughts, when suitable host plants are scarce, no doubt due to their dispersal ability. Migration in *L. frustalis* was first noted by Taylor (1940, 1962), who pointed out the similarities to *L. sticticalis* (Injac 1977; Johnson 1969; Popov 1976a).

Predictably, the seasonal abundance of moths can be correlated with the growth cycles of Karoo bushes of all species reported by Roux (1968) which are themselves influenced by rainfall (Roux 1966). But on a monthly basis there is no correlation (rank coefficient = 0,03). The correlation between moth abundance and pentzias only may be closer (Vorster, unpublished). Overall, moth flights are sporadic, a characteristic which *L. frustalis* shares with *L. sticticalis* (Belov & Balaev 1976; Camprag 1976; Knor & Tibatina 1978; Novinskii 1977; Orischenko 1976; Petrukha & Tribel' 1975; Polyakov & Chenkin 1979; Polyakov *et al.* 1977; Poplavskii 1975; Swailes 1960; Tribel' 1978).

In monthly and seasonal catches, females of *L. frustalis* usually outnumbered males (overall ratio 1,27 : 1), which agrees with the conclusion of Wolmarans (1968). From day to day, however, the ratio varied and was often reversed, even in large populations. The variability is not as marked as in *L. sticticalis*, in which migrating populations often consist almost entirely of either sex (Pepper & Hastings 1941). The census of *L. frustalis* dormant larvae (Section 6), yielded about equal numbers of females and males (overall ratio 0,96 : 1). The fact that proportionately more females are caught in light traps suggests that polymorphism for migration, similar to that reported by Adesiyun & Southwood

(1979) may also be important in this species.

Moth abundance in *L. frustalis* does not predict egg numbers. Wolmarans (1968) showed that reproduction is influenced by climate and his finding that mating is highly variable in field populations is endorsed. In this way *L. frustalis* resembles *L. stictical is* (Endakov 1979; Knor & Tibatina 1978; Pepper 1938; Pepper & Hastings 1943; Popov 1976b). Dissections of the reproductive systems and genitalia of adults caught in light traps revealed that characters which designate newly-mated females deteriorate after a time so that mating history is practically indeterminable (see below). Criteria to distinguish between 'fresh' and 'old' matings are necessary to define mating status and evaluate its obviously important role. Mating frequency increases during rainy weather (analysis of data in Wolmarans (1968) and this study) but the significance of multiple matings and how long sperm remains viable is not understood.

The events which lead to oviposition are complex (e.g. Dingle 1972; Johnson 1963, 1966, 1969; Kennedy 1961) and require further study in the case of *L. frustalis*. Until then predictions of larval outbreaks will remain intuitive. It is possible to say what veld is likely to be attacked (Section 7), but not when. So light-trap measures of moth abundance are of no predictive value in forecasting the number of eggs that will be laid during a season or in predicting when larval outbreaks may be expected.

HOST SELECTION

Many of the authors listed by Annecke & Moran (1977) ob-

served that pentzias are the most important host plants of *L. frustalis*. Certainly they are the commonest hosts but the relative importance of other species (some of which have been identified, notably by J.S. Taylor) has received little attention. Taylor (1940) observed that single *L. frustalis* eggs, and small clusters of eggs, are laid on the underside of host-plant leaves, although eggs are laid also on other parts of the foliage, flowers and stems. Marais (1955) suggested that eggs are laid on the tallest structures in the environment, including non-hosts (particularly grass), fence posts and so on. Presumably, the larvae emerging on non-hosts starve and this was used to argue in favour of a greater grass component in the Karoo. In laboratory cages, oviposition is haphazard. However, completely indiscriminate oviposition is unlikely in the field, more so because of the aromatic nature of Karoo bushes.

During the present study, low-density larval populations of *L. frustalis* (endemic) were found exclusively on pentzias, the plants being sometimes isolated or in small patches. Isolated larvae were not found on other plants, even when moths were abundant beforehand. Feeding larvae were found exclusively on healthy, vigorous plants and sometimes, as noted by Marais (1955), these are lacking for long periods during droughts.

Epidemic *L. frustalis* larval outbreaks are spectacular and led Taylor (1940) to equate the resulting damage with that of severe droughts. This amounts to near-total defoliation of food plants over hundreds of square kilometres. Under such epidemic conditions larvae disperse and feed on alternate food plants as well as on pentzias. In all situations where this was seen (De Aar, Hanover and Richmond districts) defoliated pentzias were

invariably found nearby; when the alternate food plants were isolated from pentzias they were never damaged. Clearly, populations must build up on pentzias and only under those circumstances do they 'spill over' onto alternate food plants and sometimes onto non-hosts. This 'forced' polyphagy is a feature of epidemic populations of *L. frustalis*.

All known *L. frustalis* host plants and non-host plants found in the Karoo are listed in Table 15 (Appendix 3) and classified according to their status as favoured or non-favoured food for the caterpillars. This is a tentative classification founded on field observations supplemented by preliminary laboratory screening (see General Materials and Methods). In the diverse plant communities of the Karoo, the susceptibility of plants must be influenced by associated species, as is their palatability to stock (Botha 1981). Also, the procedure for ranking food plants is risky, for many reasons expounded in text books of biological weed control and by Zwölfer & Harris (1971), mainly because food quality (see for example Dempster & Lakhani 1979; Derr *et al.* 1981; Lakhani & Dempster 1981; Webb & Moran 1978) and larval age are disregarded. The vagaries of screening plants for palatability are well illustrated by some anomalous results. For example, in laboratory trials (including preference tests), *Felicia muricata* emerges as a major host plant but was avoided as a host plant in the field by *L. frustalis* larvae.

LARVAL HABITS

Individual *L. frustalis* larvae spin flimsy silken tunnels and webs around their feeding sites. These are near the periphery of host plants, the site of most new growth. It is not known how

many such shelters are constructed by a larva during its lifetime. The larvae are extremely active; when disturbed they retreat rapidly into their shelters. Feeding larvae utilise flowers, leaves and the bark of new growth. Young larvae feed superficially, which leads to desiccation of leaves. This damage is easily overlooked in the field, especially if the larvae are no longer present, since the symptoms resemble those caused by severe droughts. The defoliation caused by older larvae, however, is unmistakable, as are the webs (frontispiece).

L. frustalis larval cases are constructed in the soil mainly near the main stems of food plants (Section 6). Subsequent census data will show that less than 50% of feeding larvae reach maturity and construct larval cases. Rarely encased larvae are found beneath non-hosts. The narrower host range at lower larval densities suggests that larvae disperse in search of food rather than dispersing for pupation sites - so that larval cases are mainly under plants that the larvae have fed upon. Importantly, in epidemic situations, pupation sites are not necessarily related to larval food-plant preferences. Negligible numbers of cases (less than 1% in 189 samples) were found in bare ground and under grass between food plants. Cases examined *in situ* (directly and by sampling at different depths) in the field were in the upper 4 - 5 cm of soil and positioned upright, with their open ends level with the top of the soil, below the plant debris.

It has often been suggested that the larval cases of *L. frustalis* are protective. Preliminary laboratory trials show that the cases increase drought-resistance and resist flooding. The cases also serve to reduce infection by *B. bassiana*; when larvae were removed from their cases and held in sterilised sand

inoculated with the pathogen, virtually all died from the fungal infection. For protection against temperature extremes, the insulating properties of the soil itself are probably more important than those of the cases.

THE IDENTIFICATION OF *L. FRUSTALIS* FROM FIELD-COLLECTED MATERIAL

E.G. Munroe (*in litt.* 1979) dismissed doubts about the correct generic name of the Karoo caterpillar. He states that *Loxostege* Hübner is correct and that *Phlyctaenodes* Newman is preoccupied as a genus of Coleoptera. Other lepidopterans found during the census do not resemble *L. frustalis* stages so that brief descriptions of the life-history stages of the Karoo caterpillar suffice.

The EGGS of *L. frustalis* darken during development from cream through yellow and orange to almost black. They are roughly oval and moulded to the substrate. Sizes (means ± standard errors) are 0,65 ± 0,01 mm (length), 0,48 ± 0,01 mm (width) and 0,31 ± 0,01 mm (depth).

Owing to dormancy, the LARVAE of *L. frustalis* in the fourth or fifth instar are frequently found in cases. The larvae are typical pyralids (Allyson 1976). They are dark-green to black with paler dorsal, lateral and ventral stripes; the latter are the most conspicuous while dorsal markings are sometimes lacking. The integument has a shrivelled appearance. Length varies between 5 mm and 10 mm and depends largely upon the instar, but there is some overlap and size alone is not an infallible criterion for separating the instars. The prothoracic shield is dis-

tinct, usually with a white line at the site of ecdysial cleavage. So far it has not been possible to separate the sexes in the larval stage (Atkinson 1980; Hinks & Byers 1973). The above description does not apply equally to feeding larvae. The latter are more slender, smoother in appearance and generally a paler, greener colour (frontispiece).

Larval head capsules of *L. frustalis* are usually black, sometimes mottled brown, with a distinct clypeus (fig. 5).

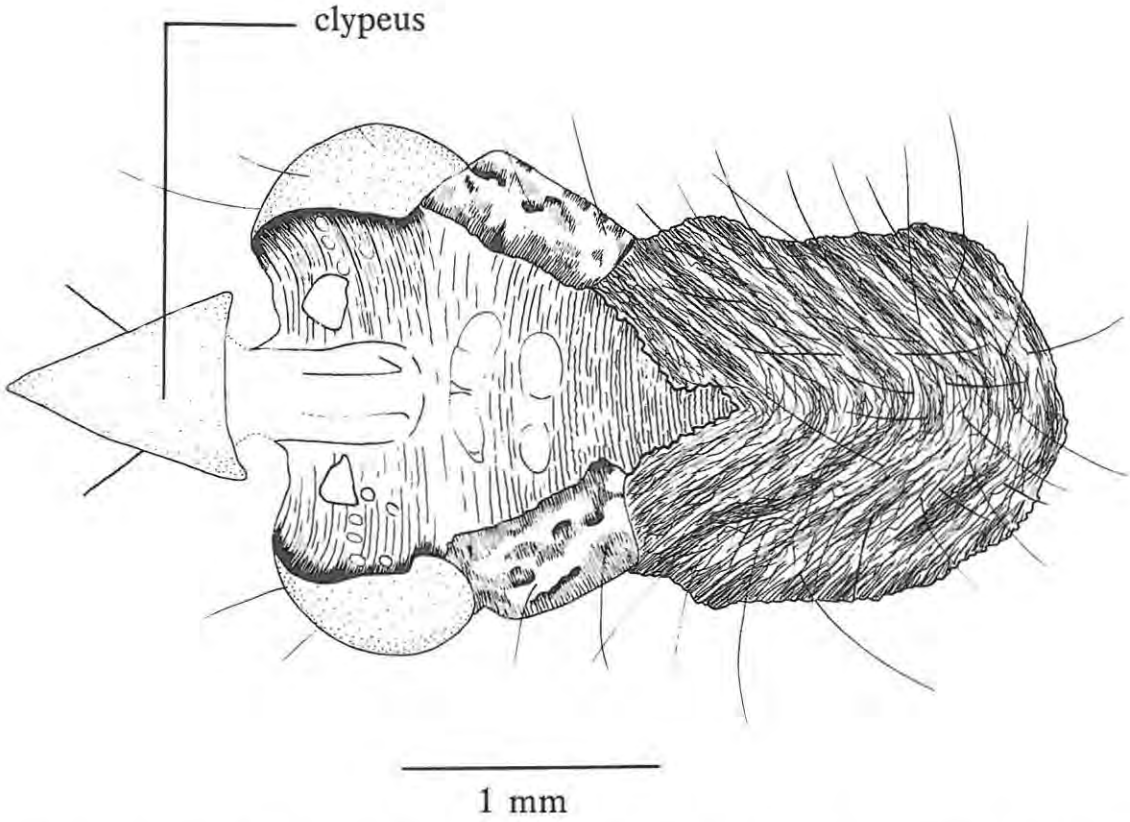


Fig. 5. Larval exuvium of a final-instar *L. frustalis* larva, showing the split head capsule and inner surface of the clypeus.

The widths of these structures are vital for separating the instars and require comment. From the linear relationships in fig. 6 it is clear that the larvae conform to Brook's Rule (often called Dyar's Rule) of geometric growth (Crosby 1973). The curves fitted to the discrete values are a convenient test of linearity and

expected values; a close fit indicates that no instars have been overlooked (Fredeen 1981; Glover 1934; Ross 1979; Wigglesworth 1965). Further, the slopes provide expected growth ratios.

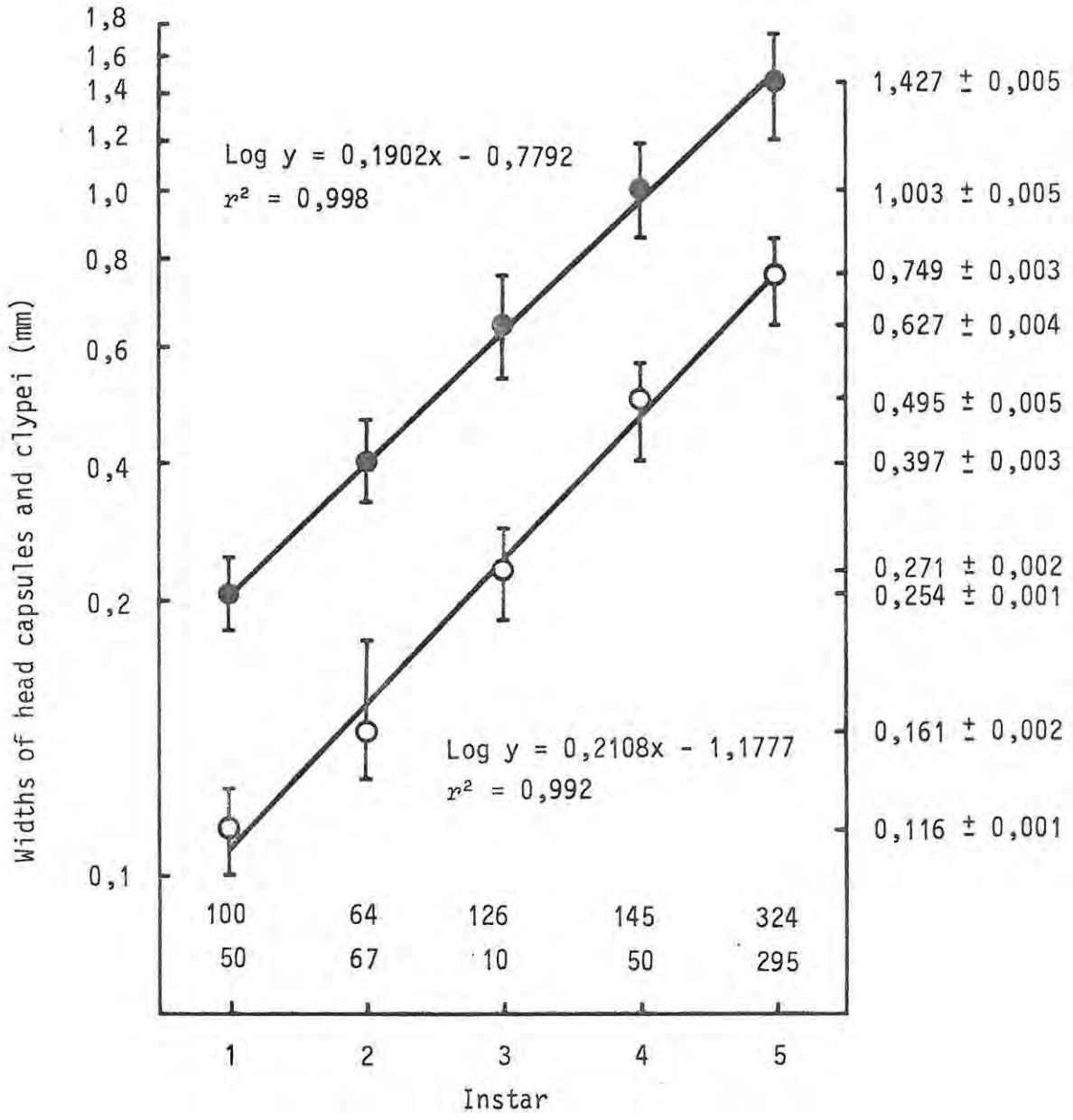


Fig. 6. Widths of head capsules (filled circles) and clypei (unfilled circles) of *L. frustalis* larvae. Means and ranges are shown. Actual means ± standard errors are on the right. Number of observations per instar are above the horizontal axis for head-capsules (upper line) and clypei (lower line).

The variation in growth ratios (Table 4) reflects the diverse growing conditions of the source material (Section 3).

Table 4. Observed and expected growth ratios of *L. frustalis* larvae, based on head-capsules and clypeus widths shown in fig. 6. Means ± standard errors are shown. Expected values are obtained from the slopes in fig. 6.

Moult	Head capsules	Clypei
1	1,5630	1,3879
2	1,5793	1,6832
3	1,5997	1,8266
4	1,4227	1,5131
Mean (observed)	1,54 ± 0,04	1,6 ± 0,1
Mean (expected)	1,55	1,62
Pooled mean (observed)	1,57 ± 0,05	
Pooled mean (expected)	1,59	

A few factors which contribute to the variation are recorded in Table 5. Although many of the tabulated differences are statistically significant, they are too small to confound separation of the instars. Head-capsule widths are sexually dimorphic in some lepidopterans (McNeil 1978), but not in *L. frustalis*. Differences between clypeus widths in fifth-instar larvae were significant ($P > 0,5$: 48 degrees of freedom). The mean head-capsule width of 1,427 mm (fig. 6) for fifth instars is within the limits of those recorded for other *Loxostege* spp. (Allyson 1976, 1981), but smaller than in most. The value is probably an underestimate, as suggested by the slight departure from linearity, and further, the range of growing conditions are bound to be sub-optimal on average.

Table 5. Some factors which influence the widths of *L. frustalis* larval head capsules and clypei. Means ± standard errors (mm) are shown. *n* = number of observations. Significance of *t* at $P < 0,05$ (*) and $P < 0,01$ (**)

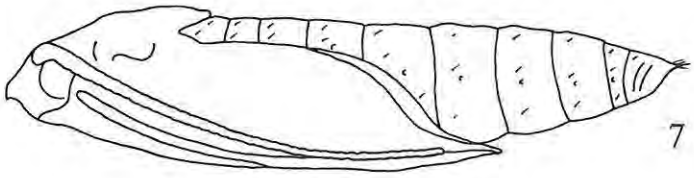
Structure/ Instar	Groups compared		*t*
n			
A) Parasitism by *Ch. curvimaculatus*			
	UNPARASITISED	PARASITISED	
Head capsule/ 3	0,605 ± 0,009	0,644 ± 0,006	3,68**
n	33	45	
Head capsule/ 4	0,941 ± 0,011	0,962 ± 0,008	1,6
n	38	53	
Clypeus/ 3	0,266 ± 0,004	0,280 ± 0,004	2,49
n	33	46	
Clypeus/ 4	0,462 ± 0,007	0,479 ± 0,004	2,24*
n	38	86	
B) The source of material parasitised by *Ch. curvimaculatus*			
	LIVE HOSTS	REMAINS	
Head capsule/ 4	0,962 ± 0,008	0,8715 ± 0,0002	7,74**
n	53	33	
Clypeus/ 4	0,483 ± 0,005	0,472 ± 0,006	1,26
n	53	33	
C) Parasitism by *M. maraisi*			
	UNPARASITISED	PARASITISED	
Head capsule/ 5	1,458 ± 0,006	1,378 ± 0,012	6,72**
n	150	63	
Clypeus/ 5	0,753 ± 0,003	0,714 ± 0,006	4,43**
n	212	26	
D) Laboratory rearing			
	FIELD	LABORATORY	
Head capsule/ 5	1,427 ± 0,005	1,287 ± 0,018	7,91**
n	324	26	
Head capsule/ 4	1,003 ± 0,005	0,932 ± 0,006	9,49**
n	145	124	
Clypeus/ 5	0,749 ± 0,003	0,664 ± 0,004	18,31**
n	295	210	
Clypeus/ 4	0,495 ± 0,005	0,448 ± 0,004	5,75**
n	50	182	

Overlap between the *L. frustalis* larval instars is exceptional and virtually restricted to laboratory cultures. Fifth-instar larvae with head capsules and clypei as narrow as 1,1 mm and 0,54 mm respectively have occasionally been reared in captivity and could easily be mistaken for the preceding instar. When the 'small' larvae pupate, the pupae nearly always die. In fourth-instar larvae, on the other hand, the structures practically never exceed 1,15 mm and 0,58 mm. It is on the basis of these results that 1,15 mm and 0,6 mm (for head capsules and clypei) were employed to separate fourth-instar and fifth-instar larvae, in the absence of other proof, for analyses of the census material (Section 6). The values were reliable in practice and their accuracy is supported by an application of Brook's Rule: when multiplied by the overall growth ratio of 1,57 (Table 4), the values approximate the maximum widths encountered to date. Laboratory material is excluded from the measurements of fourth-instar and fifth-instar larvae shown in fig. 6. The census data are therefore unaffected by the above exceptions. Assumptions about geometric growth and the number of larval instars are risky (Goettel & Philogène 1979). There is, however, no reason to anticipate meaningful departures from the given values.

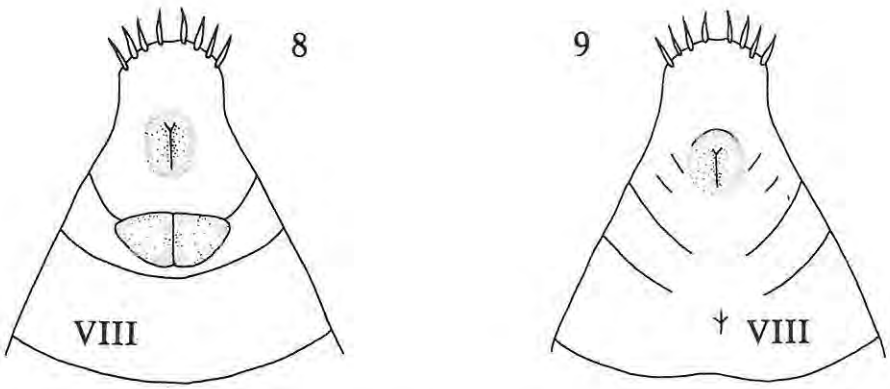
Clypeus widths are also presented since they are in some ways more useful than those of head capsules. From fig. 6 it is obvious that the two are correlated (r = 0,99). Predictably a t-test between their growth ratios revealed no differences ($P > 0,5$). The high correlation hides a tendency for the clypei of small fifth-instar larvae to be disproportionately large. They are seldom less than 0,6 mm wide and there is less size overlap

and therefore clypeal widths are more useful than head-capsule widths. Clypei are also less subject to distortion when hosts are destroyed by *Ch. curvimaculatus* (Table 5-B). Such distortion may be caused by other natural enemies and even be manifest in larval exuviae. A distinct advantage of clypeal measurements is that they can be measured in larval exuviae (fig. 5) and often in damaged head capsules.

The PUPAE of *L. frustalis* (fig. 7) are a dull-yellow colour; they and their exuviae are unlike any parasitoid stage. The method of Butt & Cantu (1962) is suitable to separate the sexes (figs 8 - 9). Remains left by dipterous pupal parasitoids, however, often resemble *L. frustalis* pupal exuviae. To avoid misinterpretation, parasitoid remains or moth scales must be searched for.



5 mm

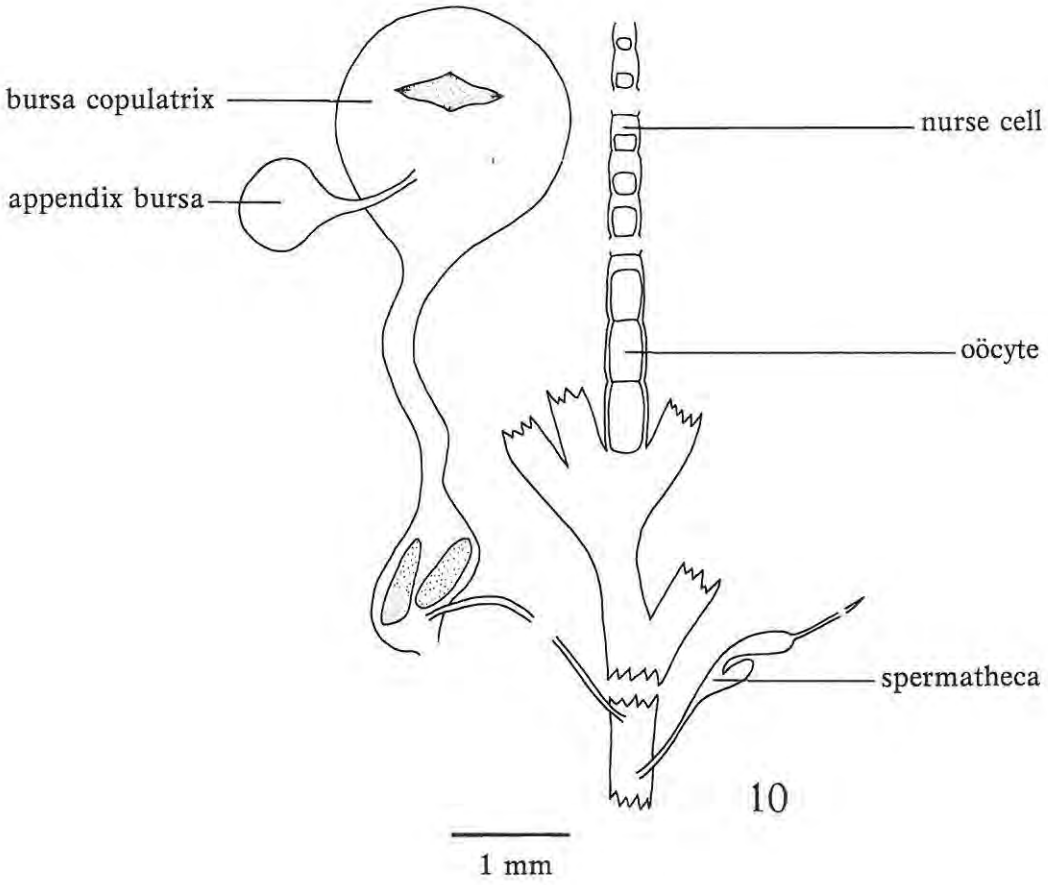


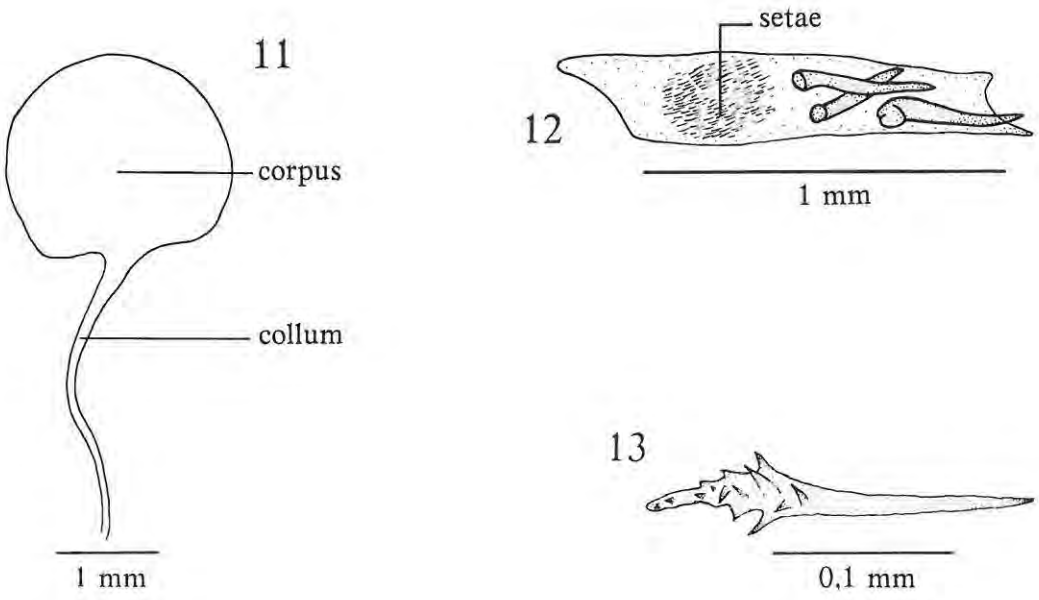
1 mm

Figs 7 - 9. *L. frustalis* pupae. 7. Female. 8 - 9. Terminal abdominal segments, ventral aspects. 8. Male. 9. Female.

The ADULTS of *L. frustalis* are characteristically marked moths (frontispiece). The genitalia are typically lepidopteran and markedly different in the sexes, and further, the frenulum is one-spined in males and two-spined in females. Moth scales are usually left at the opening of larval cases when adults emerge from them.

A number of characteristics of *L. frustalis* adults provide information about the mating status of either sex. Some of these were employed by Wolmarans (1968) and are briefly reviewed. The terminology is that of Callahan & Chapin (1960) and Wolmarans (1968). The only infallible proof of mating in *L. frustalis* females is the presence of spermatozoa in the spermatheca (fig. 10): i.e. they impart a silvery (mother-of-pearl) appearance to the otherwise flimsy, transparent structure. It is impractical to search for spermathecae in routine work, and other criteria are usually more suitable. In newly-mated females the corpus of the spermatophore (fig. 11) makes the bursa copulatrix swollen, turgid and white (fig. 10), while in virgin females it is collapsed and dull yellow. Within a few days the spermatophore is reduced to, at most, remains of the collum, and the bursa is similar to that in virgins, a comparable situation to that reported by Elliot & Dirks (1979). After mating a yellow-orange substance is present in the appendix bursa (fig. 10). This substance is of unknown function and probably originates in the male reproductive system (accessory glands?). It too is sometimes lost but persists for longer than the spermatophore and is often a useful criterion to detect mating. Conspicuous reddish-brown setae from the males (see below) are usually - but not always - transferred to the bursa during mating. The setae are no longer





Figs 10 - 13. Parts of the reproductive system and genitalia of *L. frustalis*. 10. Female reproductive system. 11. Spermatophore. 12. Aedeagus. 13. Seta from aedeagus.

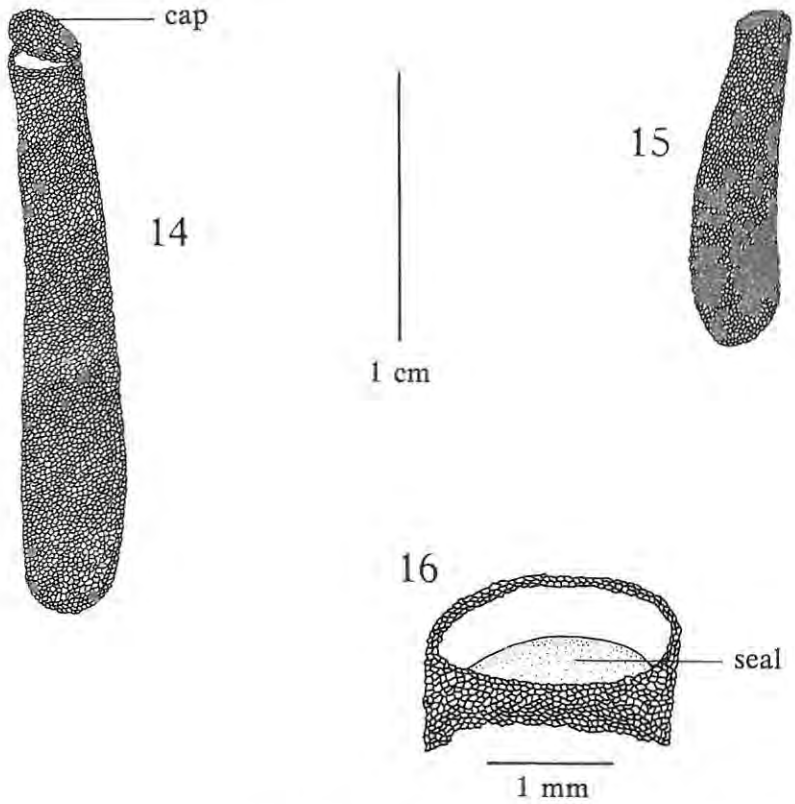
evident once the spermatophore is reduced. These three criteria are all conclusive evidence of mating. Lack of these criteria means that females either mated some time ago, or that they are virgins.

In sexually mature *L. frustalis* males, the spermatozoa causes a silvery appearance in the reproductive system similar to that in the spermatheca and the sperm cells are easily seen in a drop of 5% aqueous eosin. The red setae are in a dense cluster inside the aedeagus (figs 12 - 13) on the inner surface of the spermatophore duct and are transferred during the first mating on the outside of the spermatophore. The setae are a good indicator of male virginity. Multiple mating in males is indicated by the loss of setae from the aedeagus and their absence in the bursae of some newly-mated females.

The ovarioles of *L. frustalis* are typically lepidopteran (fig. 10) and two options are open to categorise oöcyte development. Wolmarans (1968) used the diameter of individual oöcytes. A more simple criterion of potential use is the size (volume) of the oöcytes compared to the nurse cells in the polytrophic ovarioles (terms as in Wigglesworth 1965) - in unstained ovarioles the oöcytes are opaque as opposed to the transparent nurse cells.

The LARVAL CASES of a few hitherto unidentified lepidopterans are easily confused with those of *L. frustalis*, hence the inclusion of negative characteristics in the description below. The larval cases of *L. frustalis* (figs 14 - 16) are tubular with the lower end rounded, and taper slightly towards the flat upper (open) end. They are usually straight, at most slightly curved. Size varies mainly according to the larval instar; they are 10

mm to 40 mm (average about 25 mm) long and about 4 mm wide.



Figs 14 - 16. *L. frustalis* larval cases. 14 - 15. Constructed by fifth-instar and fourth-instar larvae. 16. Open end with cap removed.

Internal diameters are slightly wider than the larvae. As with the larvae, the sizes of cases do not always indicate the larval instar. Two layers are distinguishable in the larval cases. The outer layer consists of soil particles (generally the finer component) closely spun together with silk and is without faecal pellets or detritus. At the open end, loosely woven silk and grit form a distinct cap. The inner layer is a smooth, closely woven (waterproof) sheath loosely joined to the outer layer. It is sealed about 1 mm below the top edge of the outer layer and it is torn by moths or parasitoids when they emerge. The larval cases tear easily and are never leathery, brittle, soft and spongy,

resilient or ductile. Compared to other lepidopterous larval cases retrieved from the soil in the Karoo, the *L. frustalis* cases appear smooth.

5. THE BIOLOGY OF *L. FRUSTALIS* NATURAL ENEMIES

In order to interpret the contents of *L. frustalis* larval cases it is essential to understand the development of the *L. frustalis* natural enemies in relation to that of their host (fig. 17). Salient life-history features of the *L. frustalis* natural enemies are set out in Table 6 and the host-parasitoid relationships, based on rearings from hosts held singly, are shown in fig. 18. Some of these relationships have been recorded by Möhr (1980) and Prinsloo (1980a, 1980b).

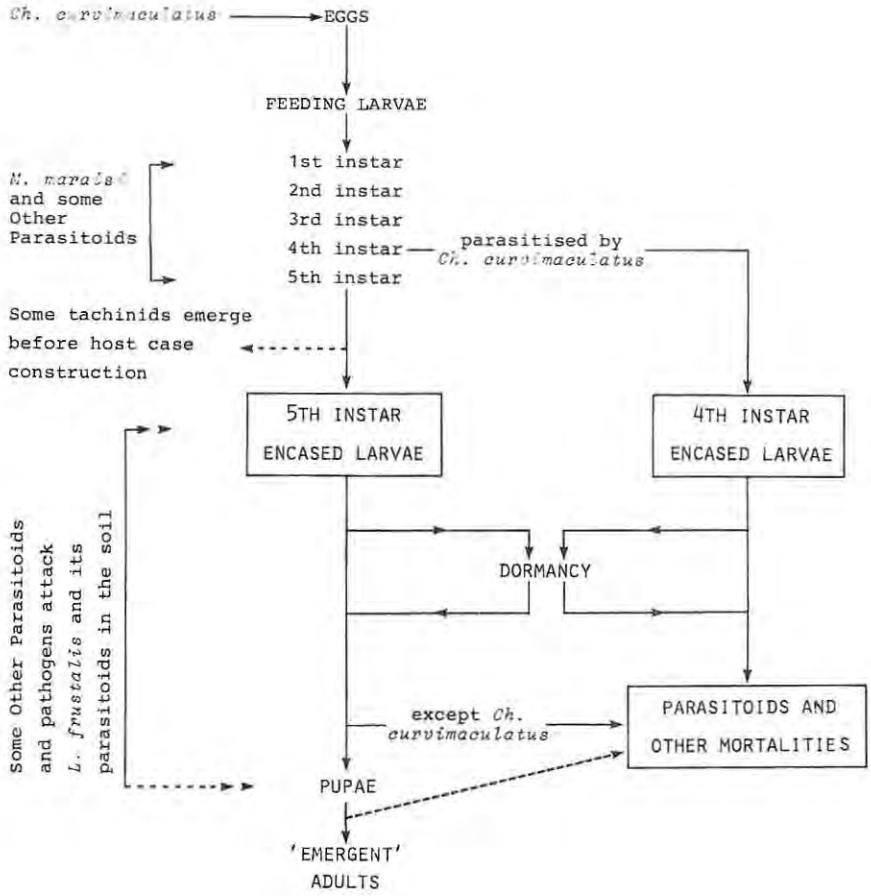


Fig. 17. Salient features of the life history of *L. frustalis* and interactions with its natural enemies. The bold type shows the material which is the subject of the census in this study. The broken lines indicate infrequent events. 'Other Parasitoids' and 'Other Mortality' are defined in Section 6.

Table 6. Biological features of *L. frustalis* natural enemies. Partly after Annecke & Moran (1977).

	L. frustalis stages attacked	Host stages killed	Larval arrested development		Stages which select hosts	Oviposition in eventual host	Superparasitism recorded	Stages when supernumeries die
			First instar	Final instar				
PRIMARY PARASITOIDS								
Chelonus curvimaculatus	Eggs	Encased larvae	Yes	No	Adults	Yes	Yes	Eggs
Cremmops frustalis	Feeding larvae	Encased larvae	Yes	No	Adults	Yes	?	?
Macrocentrus maraisi	Feeding larvae	Encased larvae	Yes	Yes	Adults	Yes	Yes	First larval
Temelucha picta	Feeding larvae	Encased larvae	Yes	No	Adults	Yes	?	?
Tachinidae	Feeding larvae	Fully-fed larvae, encased larvae	Yes	Yes	Adults	Yes	Yes	Eggs?
HYPERPARASITOIDS								
Perilampus rostratus	Feeding larvae	Pupae	Yes	No	First larval	No	Yes	First larval
Peltochalcidia capensis	See text	See text	?	Yes	?	?	?	?
Stictopisthus breviscapus	Feeding larvae?	Mature larvae	Yes	No	Adults	No	?	?
Exhyalanthrax flammiger	See text	See text	No?	Yes	First larval	No	?	?
E. lugens	See text	See text	No?	Yes	First larval	No	?	?
Geron sp.	See text	See text	No?	Yes	First larval	No	?	?
Spogostylum incisurale	See text	See text	No?	Yes	First larval	No	?	?
HOST RELATIONSHIPS UNKNOWN								
'bombyliid sp.'	Encased larvae?	Encased larvae, pupae	?	Yes	?	?	?	?
PATHOGENS								
Beauveria bassiana	Fully-fed larvae in soil.	Encased larvae	-	-	-	-	-	-

The *L. frustalis* parasitoids (primaries and hyperparasitoids) can complete their development in a few weeks, but all may enter a period of dormancy, during the first instar, in sympathy with their host. The duration of their life cycles is therefore variable and, as in their host, is unpredictable.

Although the main features of the biology of the natural enemies are given in figs 17 and 18 and in Table 6, some comments on the biology of each species are necessary. These are features which need to be explained in order to interpret the census data (Section 6).

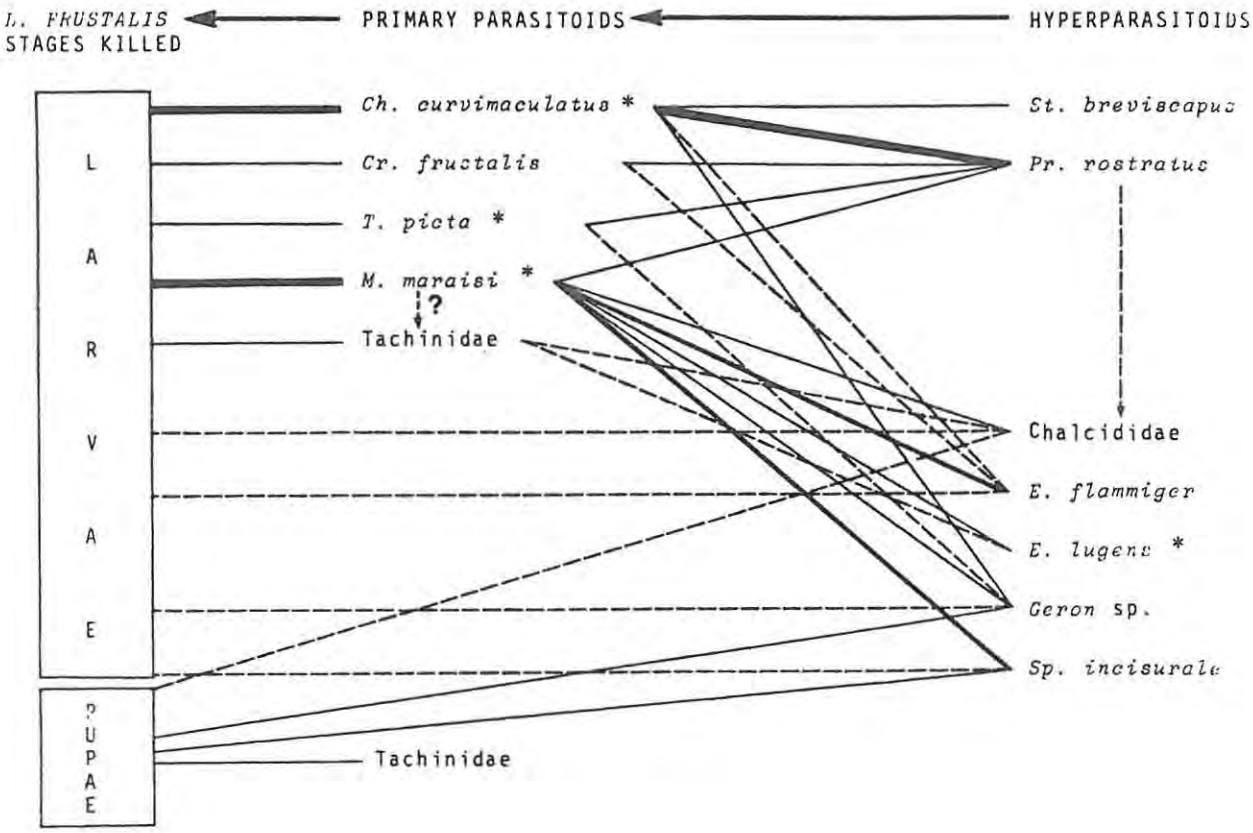


Fig. 18. Host relationships of *L. frustalis* parasitoids. Thick lines indicate common relationships. Broken lines indicate relationships determined from immature parasitoid stages. Arrows point to primary hosts. Parasitoids marked with an asterisk are known to occur on hosts other than *L. frustalis*.

THE PRIMARY HYMENOPTEROUS PARASITOIDS: *Chelonus curvimaculatus*, *Cremnops frustalis*, *Macrocentrus maraisi*, *Temelucha picta*.

Ch. curvimaculatus oviposits in *L. frustalis* eggs, but the rest of the listed primary hymenopterous parasitoids oviposit in feeding larvae. They all remain as endoparasitoids in the FIRST LARVAL INSTAR until host cases are completed. Within dormant *L. frustalis* larvae a further period of facultative dormancy follows, after which an individual parasitoid larva develops to destroy the host larva and construct a cocoon (strictly, a larval case before pupation but 'cocoon' is used to avoid confusion with host larval cases) within the host larval case. When parasitoid development is completed in the cocoons the adults chew holes in the cocoons and break the seals of host cases to escape.

Only *M. maraisi* requires additional comment. It is exceptional insofar as the development of MATURE LARVAE may also be arrested. Thus Annecke & Moran (1977) list the following developmental options that follow case construction by the hosts:

'(i) Firstly, the parasitoid larva may develop rapidly and independently within the host without any period of arrested development.

(ii) Or, the parasitoid larval development is dictated by the pattern of development in the host, that is to say, development of the *first instar* parasitoid larva is arrested for up to three years depending on developmental delays in the mature host larva; then prior to pupation of the host, the parasitoid larva develops rapidly, devours the host, forms a larval case and then a cocoon within the larval case of the host, and emerges as an adult within a few weeks. In this synchronous developmental pattern *M. maraisi* resembles *C. curvimaculatus*.

(iii) Alternatively, the *mature* larva of *M. maraisi* after deve-

lopment in the host and after devouring the host and forming its own larval case within that of the host, may *independently* enter a period of arrested development which may last up to 3 years. In these circumstances the mature larva of *M. maraisi* must respond independently to environmental cues that determine the onset of pupation. Emergence of the adult parasitoid occurs shortly after this. In no case has development in *M. maraisi* been arrested for more than approximately four years.'

The period of dormancy in first-instar *M. maraisi* larvae was overestimated (Marais 1955). *M. maraisi* merely overwinters in the first larval instar (see also (viii) under 'host relationship' below) and this accounts for the developmental options. Dormancy in the first larval instars of *Macrocentrus* spp. is common (Allen 1962; Daniel 1932; Fink 1926; Haeussler 1932; Mokrousova 1976; Putman 1963) and has been reported to occur also in eggs (Wishart 1946), but no other reports of dormancy in mature larvae have been found. The available evidence suggests that *M. maraisi* is unique in this respect. The further development of these mature larvae of *M. maraisi* is unclear. Synchrony between *L. frustalis* and *M. maraisi* populations is indicated by high correlations between moth flights and light trap catches of *M. maraisi* adults reported by Wolmarans (1968). Current work, comprising light-trap records over four seasons suggests that, like its host, *M. maraisi* adults occur throughout the summer but mainly during autumn.

TACHINIDAE (primary parasitoids)

As a group the tachinids develop similarly to the primary hymenopterous parasitoids except that eggs are oviposited topically and hosts are sometimes destroyed before case construction

(Marais 1955), and sometimes after pupation. They resemble *M. maraisi* in that dormancy occurs in the first AND final larval instars, the latter in puparia (Marais 1955). It is not known whether different developmental options of host destruction and dormancy occur in individual species.

PERILAMPUS ROSTRATUS (hyperparasitoid)

Perilampids are known to oviposit on the host plants of their primary or secondary hosts and that after hatching the motile planidia (first-instar larvae) enter their hosts through the integument (Clausen 1940; Greathead 1963; Purrington 1979; Smith 1917; Tripp 1962). Presumably *Pr. rostratus* behaves similarly - oviposition on leaves and hatching have been observed in captivity but not the entry into *L. frustalis*. Further development of *Pr. rostratus* is similar to that reported for congeners by the above authors. In the *L. frustalis* haemocoel the planidia (often several per host) remain apart from their eventual (primary) hymenopterous hosts whilst the latter are in the first larval instar. Development of the planidia is therefore attuned to that of the primary parasitoids. The planidia enter growing *Ch. curvimaculatus* larvae in a way not yet seen. When the host (*Ch. curvimaculatus*) is about to pupate the planidia are near the integument and become ectoparasitic at host ecdysis. One planidium then develops - the rest are lost, probably through cannibalism - on the host pupa and a *Pr. rostratus* adult emerges 2 - 3 weeks later.

Pr. rostratus develops normally in *M. maraisi* until the host is a mature larva. The planidia then tend to penetrate the larval integument and appear ectoparasitic, or they become scattered about the inner surface of the host cocoon. The planidia can de-

velop on host pupae only and are unable to survive when *M. maraisi* mature larvae enter a period of dormancy. Consequently, very few *Pr. rostratus* adults were recovered from *M. maraisi*, this despite a parasitism of more than 50% (by planidia) in some populations. Because supernumery planidia are normally destroyed, their presence in remains actually indicates unsuccessful parasitism. The *Macrocentrus-Perilampus* interaction is not unique (Haeussler 1930), but uncommon. Perilampids are remarkable for the diversity of insect orders which they attack as primary parasitoids (even facultatively) or are able to utilise as primary and secondary hosts for hyperparasitic habits (Allsop 1978; Askew 1971; Baker & Pigott 1979; Bogenschütz 1969a, 1969b; Bogenschütz & Lange 1970; Charles & Roques 1977; Clausen 1940; Entwistle 1963; Goncharenko 1971; Grimble *et al.* 1971; Haeussler 1930; Hinks 1971; Kerrich 1956; Léonide & Léonide 1969; Maksimović & Schindler 1969; McLeod 1975; Peyrelongue & Bournier 1974; Purrington 1970, 1979; Russ & Rupf 1974; Sechser 1970; Simmonds 1947b, 1947c; Smith 1912; Smith 1958; Thompson *et al.* 1977; Tripp 1962; Wilkinson & Drooz 1979; Zlatanova 1968, 1970). *Pr. rostratus* is an obligate hyperparasitoid and, not surprisingly, it is polyphagous.

STICTOPISTHUS BREVISCAPUS (hyperparasitoid)

Mesochorines are known to oviposit directly in primary endoparasitoids (Clausen 1940; Coseglia *et al.* 1977; Muesebeck & Dohanian 1927). However, the position is unclear in the case of *St. breviscapus* since its first-instar larva has not been identified and consequently the development of this hyperparasitoid is only partly understood. Individual *St. breviscapus* mature larvae destroy and emerge from the mature larvae of *Ch. curvimaculatus*

and complete their development in the latter's cocoons. Like *Pr. rostratus*, *St. breviscapus* is an obligate hyperparasitoid.

BOMBYLIIDAE (hyperparasitoids)

The bombyliids listed in Table 6 as hyperparasitoids select their hosts indirectly. According to Marais (1955) they oviposit in *L. frustalis* larval cases, but away from the host, as is known to occur in other members of the group (Askew 1971; Clausen 1940).

Originally it was suggested that the planidia of bombyliids associated with *L. frustalis* are endoparasitic in first-instar *M. maraisi* larvae and that they develop in sympathy with the host until cocoons are constructed. This would require a dormant period in bombyliid planidia, and bombyliids should then be recovered in rearings and dissections of dormant *L. frustalis* larvae, but during this study this never happened - the bombyliids were collected as mature larvae or as post-larval stages. When bombyliids are present in primary parasitoid cocoons or puparia, it means that bombyliids attacked after *L. frustalis* had been destroyed by another primary parasitoid, that is, they are 'true hyperparasitoids' as defined by Smith (1916). There is no doubt that the four known bombyliid species associated with *L. frustalis* are hyperparasitoids; their recovery from primary parasitoid cocoons is proof of this.

According to Bowden (*in litt.* 1979 and in Annecke & Moran 1977)) some of the hyperparasitic relationships of the bombyliids shown in fig. 18 are unusual but explicable. However, this is not so when they appear to be primary parasitoids (fig. 18). With the exception of *E. lugens* all the bombyliids listed in Table 6 may occur in *L. frustalis* larval cases together with host larval remains, but without evidence of any other parasitoids or their

remains. Similarly, *Sp. incisurale* and *Geron* sp. sometimes appear to kill *L. frustalis* pupae. These conditions are not rigid proof of primary parasitism, but other indirect evidence also points to facultative primary parasitism in the group:

(i) When bombyliids apparently attack dormant *L. frustalis* larvae, primary parasitoids can be present only as first-instar larvae but they do not consume their host.

(ii) Primary hymenopterous parasitoids cannot be present in *L. frustalis* pupae.

(iii) The bombyliid genus *Geron* is known as a primary parasitoid of lepidopterous larvae and pupae (Bowden, cited above). The recovery of *Geron* sp. from *L. frustalis* is therefore not unexpected. In this species it is the hyperparasitic habit which is unusual. It seems, therefore, that at least some of the bombyliids associated with *L. frustalis* are facultative primary parasitoids.

The bombyliid pupae cut holes in any part of the *L. frustalis* larval cases or parasitoid cocoons and move to the soil surface. From there adults emerge, leaving behind protruding pupal exuviae.

CHALCIDIDAE (hyperparasitoids)

Development strategies in the chalcidids are diverse and in many ways resemble those of the bombyliids. The available evidence suggests that chalcidids attack after *L. frustalis* larval cases are constructed. The chalcidids were collected (albeit rarely) only as mature larvae in a state of dormancy and, like the bombyliids, they never issued from dormant *L. frustalis* larvae or their endoparasitoids. The late stages of the primary parasitoids of *L. frustalis* killed (see below) also suggest 'true hyperparasitism'. Furthermore, Marais (1955) recovered *Pl.*

capensis exclusively from collections of *L. frustalis* larval cases, not from feeding larvae. So this species at least must attack after *L. frustalis* has entered the soil. *Pl. capensis* is the only positively identified chalcidid in this study. It occurs in *M. maraisi* cocoons, indicating that larvae or pupae of *M. maraisi* were killed. More commonly it is found in characteristically hollowed-out encased *L. frustalis* larvae, in which the integument is brittle but in its original shape. The status of these 'shells' is unclear. Although the shells usually contain only a chalcidid - which suggests primary parasitism - tachinids and bombyliids are sometimes associated with similar remains and, pending further studies, the possibility of hyperparasitism cannot be ruled out. Chalcidids also develop on tachinid pharate adults and *L. frustalis* pupae and pharate adults. As with the bombyliids, facultative primary parasitism is indicated but the evidence is not incontrovertible.

PATHOGENS

The well-known (some say ubiquitous) entomophagous fungus *Beauveria bassiana* (see for example Aleshina 1978; Ferron 1978; Ignoffo 1970; Steinhaus 1963, 1964; Tanada 1964) is the only positively identified pathogen of *L. frustalis*. *B. bassiana* kills encased *L. frustalis* larvae. It is known to infect a variety of hosts mainly via the integument (Gardner & Noblet 1978; Gardner *et al.* 1979; Madelin 1966; Pekrul & Grula 1979) and presumably fully-fed larvae become infected when they enter the soil. Inoculum also occurs on plants, but to what extent it infects feeding *L. frustalis* larvae, via the integument or alimentary canal, is not known.

Laboratory trials indicate that *L. frustalis* larval cases protect the dormant larvae against infection. This is also suggested by a relatively high mortality of *L. frustalis* dormant larvae collected soon after case construction. Also, it is easy to infect larvae by letting them spin cases in inoculated soil.

Fungal epizootics are greatly influenced by climate (Ferron 1978; Franz 1961; Tanada 1964). This seems to be true for *B. bassiana* in relation to *L. frustalis*. The pathogen was most abundant in damp areas and further, the typical mycelial growth and sporulation of 'white muscardine' is not manifested under dry laboratory conditions. Probably this is why *B. bassiana* was overlooked for many years by previous workers. *B. bassiana* is capable of saprophytic growth (Steinhaus 1963; Tanada 1964; Weiser *et al.* 1976) and *L. frustalis* cadavers must be important sources of inoculum when the cases disintegrate.

B. bassiana kills *L. frustalis* larvae parasitised by obligate primary parasitoids - only for *Cr. frustalis* has difficulties in the recognition of parasitoid remains prevented confirmation - as well as the hyperparasitoid *Pr. rostratus*. A variety of micro-organisms (pathogens and others) occur together in *L. frustalis* larvae with typical *B. bassiana* symptoms. Mixed infections, in the words of Tanada (1964), 'may vary from coexistence to antagonism to synergism'. Besides the bacteria listed by Annecke & Moran (1977), *Aspergillus* spp., *Fusarium* spp. and *Trichoderma* spp. have also been isolated from *L. frustalis*. Some species of these genera are known to be pathogenic (van der Westhuizen *in litt.* 1977) but their role as enemies of *L. frustalis* is unknown. In all, too little information is available to know how *B. bassiana* interacts with other *L. frustalis* natural

enemies in the Karoo.

HOST RELATIONSHIPS

The host relationships of the natural enemies of *L. frustalis* (figs 17 and 18 and Table 6) are such that the following points are important when interpreting the contents of *L. frustalis* larval cases for the census.

(i) The identification of *L. frustalis* parasitoids *per se* is not necessarily a count of *L. frustalis* larval cases. Several of the *L. frustalis* parasitoids are known to occur on other lepidopterans associated with pentzias (fig. 18). Conversely, probably not all the parasitoids of *L. frustalis* have been identified. Annecke & Moran (1977) list several in their Table 2 which were not encountered during this study. *Lasiochalcidia spinigera* Steffan has been recorded from an unidentified lepidopterous pupa (Prinsloo 1980b) and may well be a parasitoid of *L. frustalis*.

(ii) Due to the opportunistic habits of the *L. frustalis* hyperparasitoids, primary parasitoids cannot be identified from the hyperparasitoids alone. Besides, the interactions shown in fig. 18 are almost certainly incomplete. In this respect interpretation is greatly simplified by the habits of *L. frustalis* primary parasitoids to construct easily recognisable cocoons inside the host larval cases. Normally the hyperparasitoids also complete their development in these cocoons.

(iii) The presence of a hyperparasitoid in a dormant *L. frustalis* larva is not proof that the host is parasitised by a primary parasitoid. *P. rostratus* planidia, for example, have been found in *L. frustalis* pupal exuviae and apparently unparasitised dormant

larvae.

(iv) The mere presence of hyperparasitoids in *L. frustalis* dormant larvae is not proof that associated primary parasitoids are suitable hosts for the hyperparasitoids. As explained above, *P. rostratus* planidia in *M. maraisi* cocoons usually create a false impression of parasitism which continues when bombyliids, in turn, destroy *M. maraisi*.

(v) The frequencies with which interactions among the parasitoids occur are not necessarily an infallible criterion of host preferences. Commenting on the host relationship of bombyliids, Bowden (*in litt.* 1979) wrote 'In general, Bombyliidae are probably best described as habitat parasitoids or predators' and further 'One would suggest that (certain bombyliids) in outbreak areas of *Loxostege* accept larvae of *Loxostege* as a "habitat", in which primary parasitoids could be expected to occur - and it would not matter very much what the primary parasitoid was'. Pending more detailed studies, this concept of 'habitat predators' - for comments about 'habitat selection' see Doutt (1959), Doutt *et al.* (1976), Mathews (1974) and Vinson (1976) - is useful for viewing the guild of *L. frustalis* parasitoids. *Ch. curvimaculatus*, for example, is the commonest host of *Pr. rostratus* - as determined by a re-analysis of Marais's (1955) data and from the census data collected during this study, which revealed rates of parasitism of up to about 80% - but there is no evidence that it is the most suitable host, only that it is the most available. Similarly with the bombyliids associated with *L. frustalis* - at certain times of the year *M. maraisi* mature larvae (dormant) are more abundant than the remaining parasitoids of *L. frustalis* or even the host itself.

(vi) Multiple parasitism and superparasitism are sometimes encountered in dormant *L. frustalis* larvae and results from the lengthy dormant period in first-instar parasitoid larvae (fig. 17).

The consequences of MULTIPLE PARASITISM between *L. frustalis* parasitoids depicted in fig. 19 were inferred from dissections of *L. frustalis* host remains left by parasitoids and records of natural enemies other than *Ch. curvimaculatus* from fourth-instar *L. frustalis* hosts - i.e. hosts initially parasitised by *Ch. curvimaculatus* as explained in (vii) below. In fig. 20 the fate of parasitised *L. frustalis* encased larvae in the fourth instar illustrates that multiple parasitism between the natural enemies of *L. frustalis* is only partly avoided and, importantly for the interpretation of the census material, that the extent of multiple parasitism is unpredictable from one locality to the next.

Most *M. maraisi* are recovered from fifth-instar *L. frustalis* larvae: usually 80% or more, but values as low as 50% have also been recorded. The preference by *M. maraisi* for larger *L. frustalis* larvae (Marais 1955), together with the premature case construction of *L. frustalis* larvae parasitised by *Ch. curvimaculatus* (see (vii) below), probably explains why multiple parasitism involving *Ch. curvimaculatus* and *M. maraisi* is often avoided.

Multiple parasitism between primary parasitoids of *L. frustalis* affect hyperparasitoids through the replacement of suitable hosts with unsuitable ones. Several such situations can be inferred from figs 18 and 19. For example, *Pr. rostratus* nearly always dies when the eventual host is *M. maraisi* and *St. breviscapus* dies whichever parasitoid displaces *Ch. curvimaculatus*.

SUPERPARASITISM has been recorded for some *L. frustalis* para-

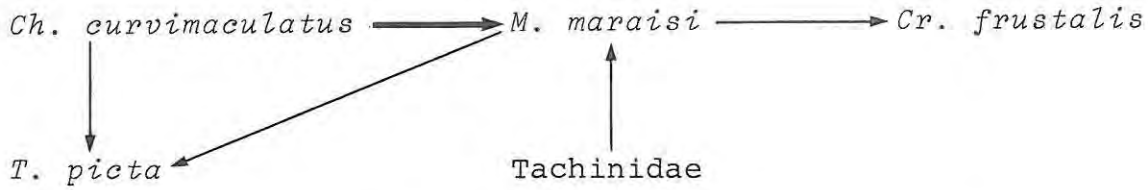


Fig. 19. The results of multiple parasitism by various parasitoids in *L. frustalis* larvae. Arrows point to the survivors after interaction between pairs of first-instar parasitoid larvae. The thick line indicates a common relationship.

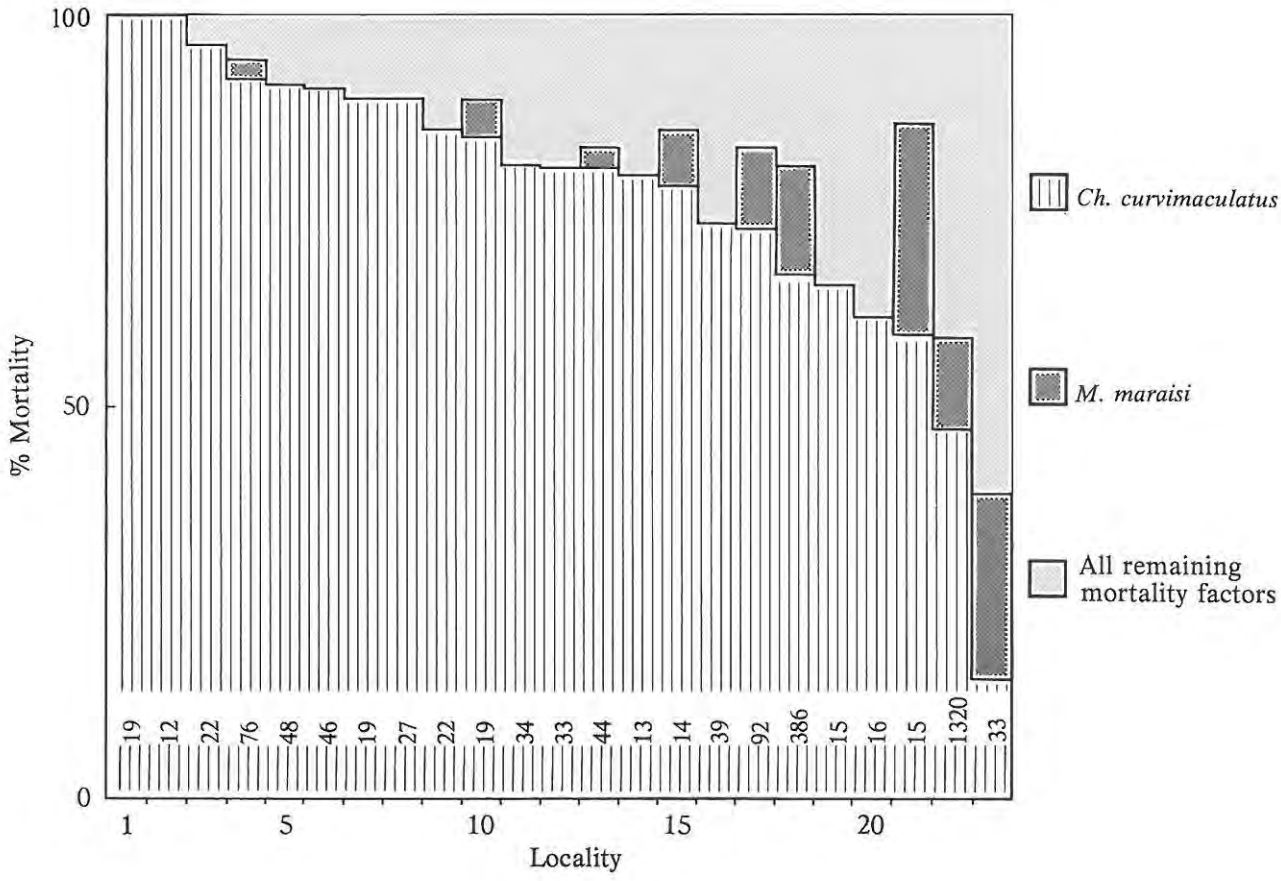


Fig. 20. The proportions of *L. frustalis* encased larvae in the fourth instar (i.e. initially parasitised by *Ch. curvimaculatus* - see text) eventually killed by (i) *Ch. curvimaculatus*, (ii) *M. maraisi* and (iii) all the remaining mortality factors, at various localities. The numbers of fourth-instar larvae for each locality are shown above the horizontal axis.

sitoids (Table 6). For the interpretation of census data, however, superparasitism is irrelevant since only one parasitoid develops to maturity in a host. There seem to be mechanisms in field populations of the *L. frustalis* parasitoids - *Pr. rostratus* is a notable exception - to avoid superparasitism.

(vii) The effects of parasitism on *L. frustalis*, particularly by *Ch. curvimaculatus*, are marked. *Chelonus* spp. commonly stunt their hosts and/or reduce the number of larval instars (Broodryk 1969; Hegazi *et al.* 1978; Jackson *et al.* 1979; Luginbill 1928; Patel & Patel 1971; Rao & Patel 1974; Rechav 1976; Rechav & Orion 1975; Simmonds 1947b). A similar change in *L. frustalis* is caused by *Ch. curvimaculatus* attack. It reduces the number of larval instars to four and shortens the feeding period (fig. 21). Thus field populations of dormant larvae fall into two distinct classes, namely fourth and fifth instars (fig. 17). By following the development of individuals in captivity it was established that parasitised *L. frustalis* hosts always remain in the fourth instar and do not develop further.

Due to multiple parasitism, however, other natural enemies apart from *Ch. curvimaculatus* also issue from fourth-instar hosts. Only *Cr. frustalis* and the tachinids appear to be restricted to the larger hosts, but too few specimens have been found for this to be conclusive. In dissections of fourth-instar *L. frustalis* larvae, *Ch. curvimaculatus* is practically always present and precedes the other parasitoids (fig. 17). It is concluded that *Ch. curvimaculatus* is the only - and invariable - cause of case construction in the fourth larval instar of *L. frustalis*. Consequently, *Ch. curvimaculatus* and *St. breviscapus* never issue from fifth-instar *L. frustalis* hosts and fourth-instar *L. frustalis* larvae always die (fig. 17).

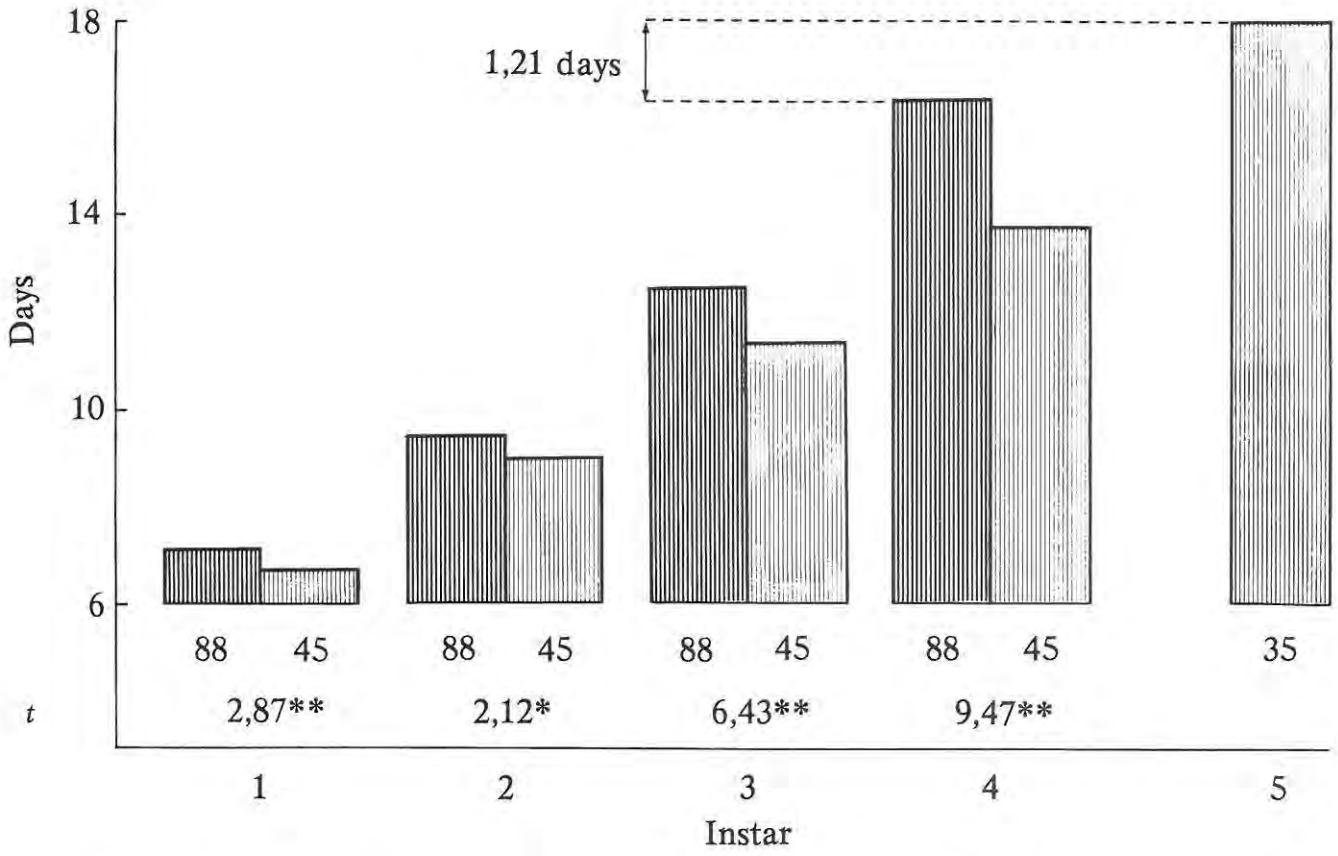


Fig. 21. Mean cumulative duration of *L. frustalis* larval instars unparasitised (light shading) and parasitised by *Ch. curvimaculatus* (dark shading). The first instar includes the egg-incubation period. The numbers of observations are shown below the columns. Values of t (above the horizontal axis) apply to non-cumulative means for individual instars. Significance of t at $P < 0,05$ (*) and $P < 0,01$ (**). Determined from the non-cumulative duration of larval development, the onset of case construction was 1,21 days later, on average, in unparasitised hosts (see text).

Ch. curvimaculatus has similar effects on several noctuids (Broodryk 1969) but potato tuber moth larvae parasitised by *Ch. curvimaculatus* appear normal (Whiteside 1980).

Unparasitised *L. frustalis* larvae, in spite of developing through a fifth instar, constructed cases on average only 1,21 days later than those parasitised by *Ch. curvimaculatus* ($P < 0,01$:

121 degrees of freedom) which construct cases in the fourth instar. In each *L. frustalis* larval instar, *Ch. curvimaculatus* significantly delayed development (fig. 21) and the third and fourth instars had bigger heads (Section 4: Table 5-A).

A few other, but minor, effects of parasitoids on *L. frustalis* growth are listed in Table 5-C (Section 4).

(viii) The development of *L. frustalis* and its natural enemies in relation to each other provides useful information about the identification and development of cohorts of *L. frustalis* dormant larvae. Because the dormancy of both *L. frustalis* and first-instar larvae of the parasitoids was mainly for overwintering, the composition of encased material (dormant and spent) in the soil changed after the onset of warmer spring weather. Healthy *L. frustalis* dormant larvae developed into post-larval stages while parasitised dormant larvae were, in effect, 'replaced' by parasitoids which developed beyond the first instar. In this respect *M. maraisi* was especially useful since the rate of parasitism in overwintered dormant *L. frustalis* larvae invariably reduced to zero in spring, and due to the further period of dormancy, mature larvae of *M. maraisi* tended to persist in the soil. Also useful were the characteristics of freshly-spun *M. maraisi* cocoons (Appendix 8) which indicated that the *L. frustalis* hosts had recently been destroyed. Similar information was provided by mature larvae of those parasitoids in which there is no dormancy after the first larval instar.

6. THE CENSUS OF *L. FRUSTALIS* LARVAL CASES

The only stages of *L. frustalis* really amenable to census are those which occur in the larval cases in the soil. The contents of the larval cases provide useful information about *L. frustalis* populations since the survival of encased larvae and post-larval stages of *L frustalis*, as well as the known natural enemies of *L. frustalis*, are manifested in the cases. In essence, the census comprised the digging of soil from beneath host plants (mainly pentzias) of *L. frustalis*, extracting the *L. frustalis* larval cases and interpreting the contents of the cases as life tables (Luck 1971; Morris & Miller 1954; Varley & Gradwell 1968) for the life-history period following case construction.

The first step in the census was to SELECT SUITABLE SITES to represent endemic and epidemic populations (Section 7) of *L. frustalis*. Details of the localities and sampling are shown in fig. 22 and Table 7. Botanical aspects and some features of the sites are recorded in Appendix 3 (Tables 15 and 16). The sizes and shapes of the sites selected depended upon the distribution of plant species. Mostly, the plots comprising the sites were roughly rectangular; their areas (Appendix 3: Table 16) were estimated from the spread of samples. The Sites 1 - 3 for the preliminary census were too big (20 - 200 ha), with excessive variation between them and further, too much time went into collecting. The smaller size of the subsequent sites (Appendix 3) was a compromise. These sites were selected for approximate 'uniformity' of the main plant species sampled and were large enough to avoid the consequences, to *L. frustalis* and the vegetation, of destructive sampling. 'Uniform' is a bold term - karroid veld tends to be patchy (Wiens 1976) on almost any scale (Acocks 1966, 1975) and if not

the dominant species, then others in the species-rich communities are clumped. Even for dominant species, apparent regularity can be misleading, as shown by the need to transform counts (Section 3).

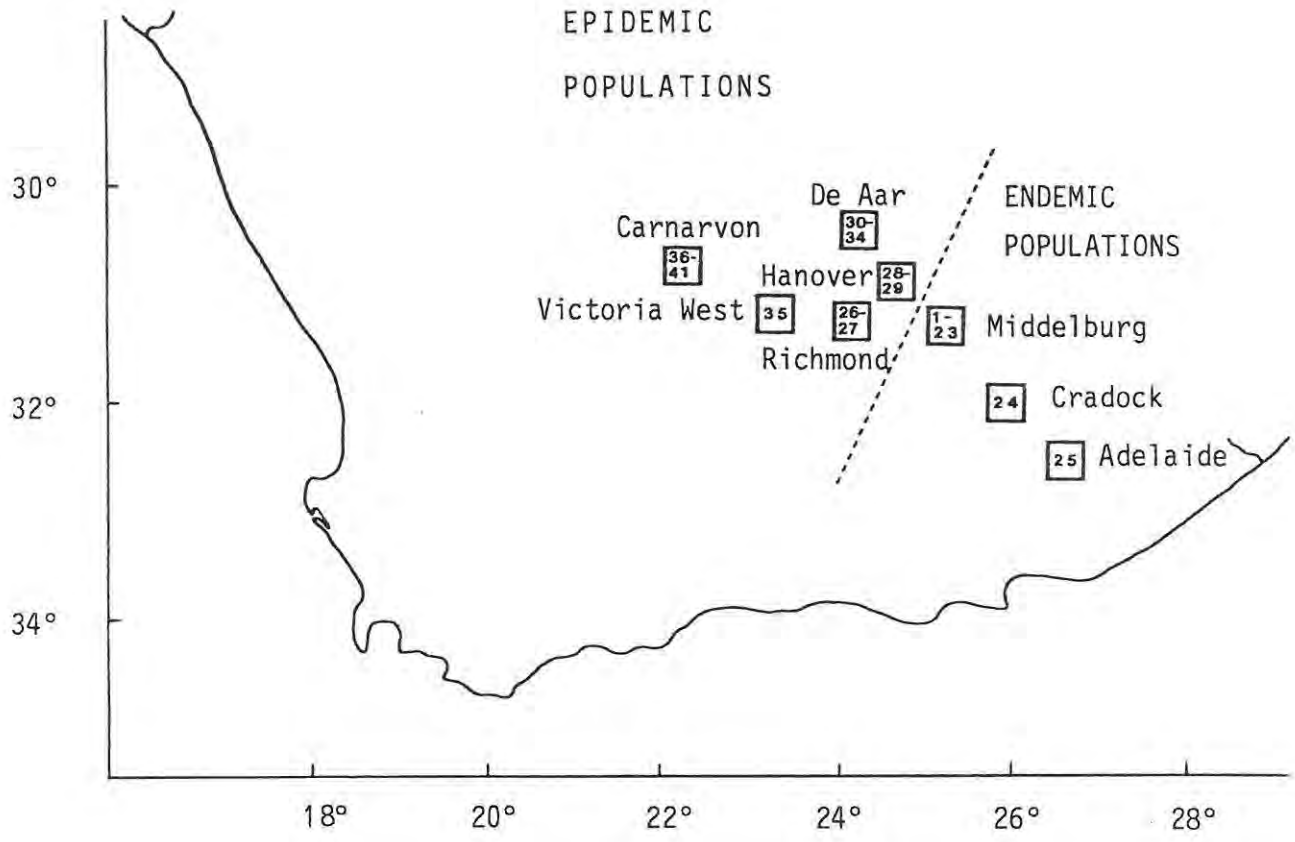


Fig. 22. *L. frustalis* census sites and site numbers. Endemic and epidemic populations (separated by the broken line) are defined in Section 7.

For the SELECTION OF PLANTS, size limits (by diameter) were set so that 'typical' plants were sampled. This had to be flexible to allow for differences in grazing, species, etc. Extraordinarily big plants in grazed veld were the exception (Appendix 3). Seedlings were sometimes plentiful, but their high mortality rate (Roux, personal communication; see also West *et al.* 1979) places

Table 7. The census of *L. frustalis* larval cases: sites and numbers of soil samples taken on each date. The numbers of rows (see text) are also given. The figures in bold type indicate two identical surveys, except where subplots (*) are identified. Censuses omitted from the partial life tables in Section 7 are shown in italics.

	Site, Plant species	Numbers of soil samples																																		
		1975				1976									1977														1978								
		S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
	MIDDELBURG																																			
1.	*E. ericoides*	50		50	20	16	16	16	16	16	16	16																								
	P. globosa	50		50	20	16	16	16	16	16	16	16																								
	P. incana	50		50	20	16	16	16	16	16	16	16																								
2.	*E. ericoides*		50	50	20	16	10	16	16	16	16	16																								
	P. globosa		50	50	20	16	16	16	16	16	16	16																								
	P. incana		50	50	20	16	16	16	16	16	16	16																								
3.	*E. ericoides*		50	50	20	16	16	16	16	16	16	16																								
	P. globosa		50	50	20	16	16	16	16	16	16	16																								
	P. incana		50	50	20	16	16	16	16	16	16	16																								
4.	*P. globosa*																											75								
	P. incana															75	75*			75*		75			75		75	75		75		75				
5.	*G. procumbens*																																			
	L. cinereum																																			
	P. globosa														75		75*			75*		75			75	75	75	75		75		75		75		
	P. incana																											75								
	R. humilis																																			
	S. calluna																																			
6.	*E. ericoides*																	75*		75		75		75		75		75				75				
7.	*P. globosa*																																			
8.	*P. globosa*																																			
9.	*C. tenuifolia*																																			
	P. globosa																																			
10.	*P. globosa*																																			
11.	*P. globosa*																																			
12.	*P. globosa*																																			
13.	*P. globosa*																																			
14.	*P. globosa*																																			
15.	*P. globosa*																																			
16.	*P. globosa*																																			
17.	*P. globosa*																																			
18.	*P. globosa*																																			
19.	*P. globosa*																																			
20.	*P. globosa*																																			
	W. saxitilis																																			
21.	*P. incana*																					25														
22.	*P. incana*																					25														
23.	*P. incana*																					25														
	CRADOCK																																			
24.	*P. incana*																						75													
	ADELAIDE																																			
25.	*P. incana*																																			35
	RICHMOND																																			
26.	*C. tenuifolia*																																			
	P. incana																																			
	P. spinescens																																			
27.	*P. spinescens*																																			
	HANOVER																																			
28.	*P. globosa*																																			
	R. humilis																																			
	W. saxitilis																																			
29.	*P. globosa*																																			
	Pl. karooicus																																			
	R. humilis																																			
	W. saxitilis																																			
	DE AAR																																			
30.	*E. ericoides*																																			
	P. spinescens																																			
	Pt. glauca																																			
31.	*P. globosa*																																			
	S. calluna																																			
	Z. incrustatum																																			
32.	*P. spinescens*																																			
	W. saxitilis																																			
33.	*P. globosa*																																			
	R. humilis																																			
	W. saxitilis																																			
34.	*P. globosa*																																			
	P. spinescens																																			
	W. saxitilis																																			
	VICTORIA WEST																																			
35.	*P. spinescens*																							25												
	CARNARVON																																			
36.	*P. spinescens*																							25												
37.	*P. spinescens*																							75												
38.	*P. spinescens*																							25				10								
39.	*Chrysocoma* spp.																											10								
	P. globosa hybrid																										25	25		25	25					25
	P. incana																											10								
40.	*P. spinescens*																						75					75								75
41.	*P. spinescens*																																			

Table 7 (cont.)

	Site, Plant species	Numbers of soil samples																													
		1978						1979												1980											
		J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	Rows
	MIDDELBURG																															
1.	*E. ericoides*																															11
	P. globosa																															11
	P. incana																															11
2.	*E. ericoides*																															11
	P. globosa																															11
	P. incana																															11
3.	*E. ericoides*																															11
	P. globosa																															11
	P. incana																															11
4.	*P. globosa*																															3
	P. incana		75			75			75			75																				39
5.	*G. procumbens*				75																											3
	L. cinereum				25																											1
	P. globosa		75			75			75			75						75											75			75	57
	P. incana																															3
	R. humilis						10																									1
	S. calluna						10	30																								4
6.	*E. ericoides*			75		75						75																				33
7.	*P. globosa*								10																							2
8.	*P. globosa*																			75												3
9.	*C. tenuifolia*																			75												3
	P. globosa																			75												3
10.	*P. globosa*														25																	1
11.	*P. globosa*														10																	1
12.	*P. globosa*														10																	1
13.	*P. globosa*														10							25										1
14.	*P. globosa*														10																	1
15.	*P. globosa*														10																	1
16.	*P. globosa*														10																	1
17.	*P. globosa*																					25										1
18.	*P. globosa*																					25										1
19.	*P. globosa*																					25										1
20.	*P. globosa*																					25										1
	W. saxitilis																					25										1
21.	*P. incana*		25																													2
22.	*P. incana*		25																													2
23.	*P. incana*		25																													2
	CRADOCK																															
24.	*P. incana*		30																													6
	ADELAIDE																															
25.	*P. incana*																															1
	RICHMOND																															
26.	*C tenuifolia*																				75											3
	P. incana											16									25											2
	P. spinescens											75	75		75	75	75	75		75	75											24
27.	*P. spinescens*														75		75															6
	HANOVER																															
28.	*P. globosa*																								75				75			6
	R. humilis																								25							1
	W. saxitilis																								25							1
29.	*P. globosa*																									25						1
	Pl. karooicus																									10						1
	R. humilis																									25						1
	W. saxitilis																									25						1
	DE AAR																															
30.	*E. ericoides*																								10							1
	P. spinescens																						25							25		2
	Pt. glauca																													25		1
31.	*P. globosa*																						10									1
	S. calluna																						10									1
	Z. incrustatum																						10									1
32.	*P. spinescens*																						25	25	25					25		5
	W. saxitilis																							25								2
33.	*P. globosa*																						25									1
	R. humilis																						25									1
	W. saxitilis																						25									1
34.	*P. globosa*																								10							1
	P. spinescens																								25							1
	W. saxitilis																								25							1
	VICTORIA WEST																															
35.	*P. spinescens*																															1
	CARNARVON																															
36.	*P. spinescens*	25																														2
37.	*P. spinescens*	75																														6
38.	*P. spinescens*		25																													3
39.	*Chrysocoma* spp.		25	25																												3
	P. globosa hybrid		25	25			25											25														9
	P. incana																	5														1
40.	*P. spinescens*						30											75														15
41.	*P. spinescens*														25																	1

them in the category of 'temporary' pioneer vegetation. If they had been included, later surveys would have been biased in favour of older plants as the seedlings died. Moreover, the number of larval cases found in the soil beneath the plants was directly related to plant size. The first plants in plots were chosen randomly and the rest spaced, more or less in rows, along the length of plots (Table 7). Plants were selected by pacing off pre-determined distances and taking the nearest plant in a random compass direction. In sparse plant populations this was impractical and the nearest plants were taken. In repetitious surveys, rows were randomly selected each time (Sites 4 - 6) or approximately the same routes were followed (for the rest). For the preliminary census (Sites 1 - 3) clusters of the three plant species (Table 7) were sampled as far as possible. Plants were ignored on the rare occasions that the area beneath their canopies was disturbed by burrowing animals. The optimum number of samples per census, to detect a twofold change in density, varied greatly between about 10 and 100. Mostly, 25 samples per row were collected, often in three rows per survey (Table 7).

L. frustalis larval cases were then COLLECTED FROM THE SOIL by carefully digging a sample-square of soil with a 20 cm wide spade, with the main stems of plants at the centres of the squares. The hole was deep enough (10 - 20 cm) to collect all the cases but the area of soil varied since holes tended to be wider (by up to 5 cm) in sandy soils than they were in compacted soils. For the preliminary census (Sites 1 - 3) the digging was much cruder and the areas even more variable. Dry-sifting, using a 4 mm mesh sieve, was the most satisfactory method of extracting the larval cases from the soil even though it took up to one man-hour per

sample. Several other sifting methods (wet-sifting, washing, dampening before sifting and blowing with compressed air) were tried and rejected for mainly pragmatic reasons.

An essential part of the census was to IDENTIFY THE CONTENTS of *L. frustalis* larval cases collected from the soil. The identification of stages of *L. frustalis* and its natural enemies are described in Section 4 (*L. frustalis)* and in Appendices 4 (immature parasitoid larvae), 5 (mature parasitoid larvae), 6 (parasitoid pupae), 7 (parasitoid adults), 8 (cocoons of primary hymenopterous parasitoids) and 9 (pathogens). The purpose of these detailed accounts is to illustrate simple, rapid methods of recognising *L. frustalis* and its natural enemies (or their remains) from samples recovered from the soil and to draw attention to key literature.

The INTERPRETATION and method used for COUNTING the contents of *L. frustalis* larval cases is set out in fig. 23. Rules to avoid 'double counts' and other misinterpretations when broken cases - caused by the digging, sifting or weathering - are collected, are listed in Table 8.

Given these methods of counting *L. frustalis* encased larvae - and the components of their mortality - in soil samples, it is now possible to describe the ANALYSIS and PRESENTATION of the census data:

(i) The census was of *L. frustalis* encased larvae that had accumulated in the soil, irrespective of the age or densities of cohorts. However, *L. frustalis* larval cases deteriorate in the soil with time (fig. 24) and may affect census values. Thus comparisons of the numbers of accumulated encased larvae within and

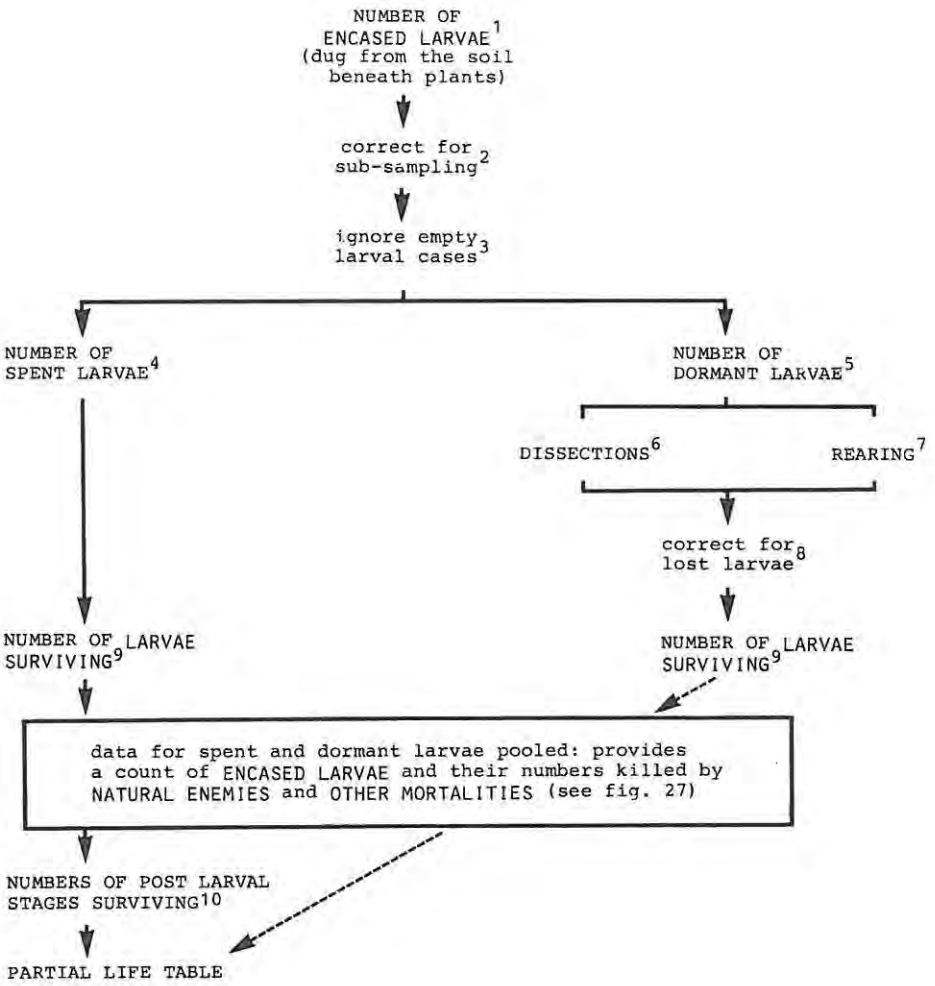


Fig. 23. Summary of the procedure to interpret and count the contents of *L. frustalis* larval cases. The method allowed census of the host and its natural enemies for the construction of partial life tables. The bold type shows the stages central to the final analysis of the census data.

1 For the interpretation of broken cases see Table 8.

2 Restricted to Sites 1, 2, 3 and 39 only.

3 Empty larval cases accounted for about 5 - 10% of the population and could not be included in the life tables. By ignoring empty cases it was assumed that they occur randomly in the soil samples, i.e. that none of the components of the life tables was over- or underestimated. Sometimes cases were holed (up to 34%) by scavengers or perhaps predators but this 'holing' was not peculiar to the empty cases or any component of the partial life tables.

4 'Spent' larvae are those cases in which *L. frustalis* survival was detectable from the presence of host remains or mortality factors.

5 Live *L. frustalis* larvae in the fourth or fifth instar. Larvae with head capsules and clypei more than 1,15 mm and 0,6 mm wide respectively were taken as fifth instar. Live *L. frustalis* pupae were counted as dormant larvae which had survived.

6 Employed as a last resort for injured larvae or for larvae in a protracted state of dormancy to detect first-instar endoparasitoid larvae.

7 By holding in gelatine capsules in the laboratory to rear *L. frustalis* or endoparasitoids.

8 'Lost larvae' were mainly those which were severely injured during collection and could, therefore, not be reliably dissected. Separate correction factors for fourth and fifth-instar dormant *L. frustalis* larvae were calculated for rows and applied to individual samples. This does not affect row totals but assumes that mortalities act independently of host densities between samples.

9 Survival to *L. frustalis* pupae was indicated by the onset of ecdysis. Larval exuviae were ignored.

10 Spent material only; restricted to censuses conducted after most dormant larvae had developed into spent larvae (see Section 5). Includes pupal parasitoids, miscellaneous pupal mortality and adult mortality through failure of adults to escape from the cases.

between sites are valid only for censuses conducted at about the same time or for recognisable cohorts of *L. frustalis* encased larvae.

Table 8. Rules for interpreting, in the absence of other material, the live or dead contents of broken[1] *L. frustalis* larval cases.

Material	Counted and included in census
HOST	
Dormant larvae	If heads present
Intact larval head capsules	No
Larval remains left by parasitoids	Chalcidids only
Larval exuviae	No
Pupae	If heads present
Pupal exuviae	If more than half present
Dead adults	No
Moth scales	No
PARASITOIDS	
Mature larvae	If head present[2]
Post-larval stages	No
Cocoons, puparia	If more than half present

[1] The definition of larval cases relates to their contents rather than the cases themselves; for practical purposes they were 'broken' only when there was a risk of double counts, which may violate some of the rules for constructing budgets (Varley *et al.* 1973).

[2] Applies to primary parasitoids which do not construct cocoons.

(ii) The highest densities of *L. frustalis* encased larvae per soil sample were near the main stems of food plants - even when the plants were unusually large, like the *P. globosa* hybrids

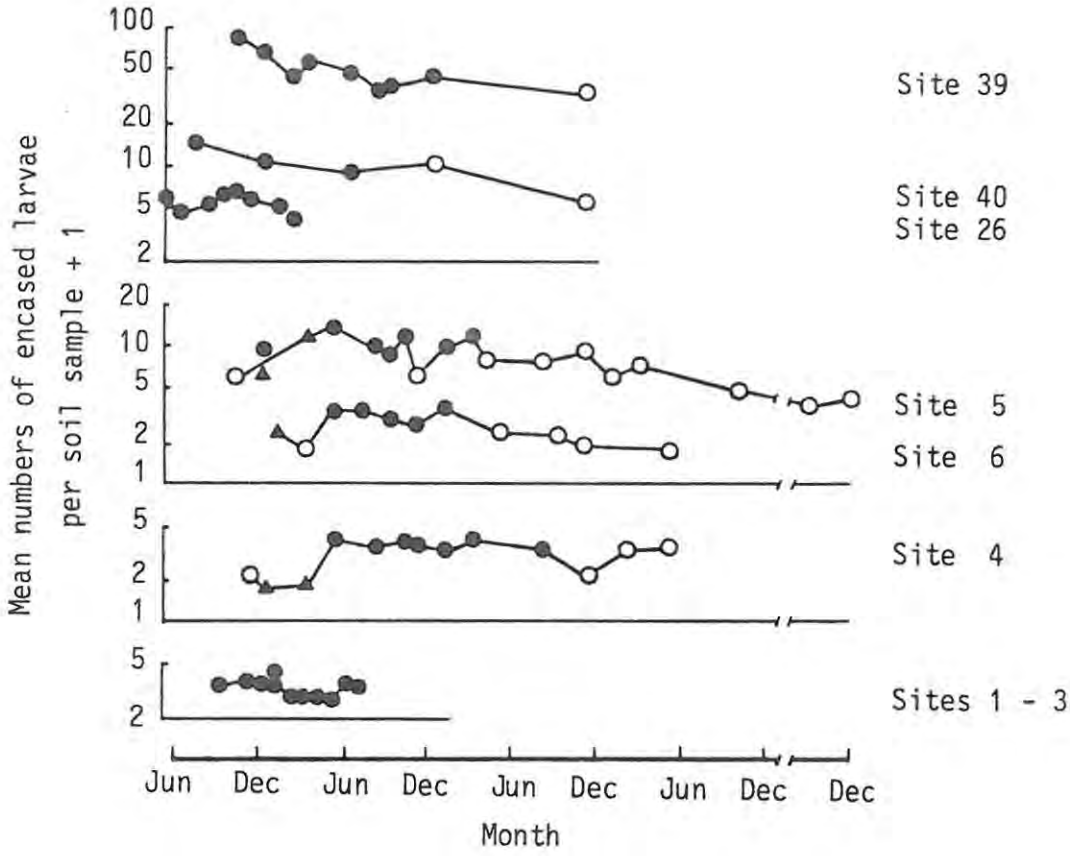


Fig. 24. The mean numbers of *L. frustalis* encased larvae per soil sample collected from pentzias on successive dates. The filled circles show data included in the partial life tables. Sub-plots are indicated by triangles.

in Site 39 (fig. 25). The total number of cases recovered from under each plant canopy, however, varied between sites (Table 9). The low recovery rates (Table 9) for samples taken at Sites 7 and 39 are due to the exceptionally large host plants (Appendix 3: Table 16): in these instances the area of soil covered by the plant canopy far exceeded the area sampled by digging. For most sites, however, the number of encased larvae in the samples generally reflected the total number of encased larvae per plant, as indicated by the positive correlations in Table 9. With the wis-

Table 9. The total number of *L. frustalis* encased larvae in the soil under each plant canopy (= per plant) and the proportion of the total recovered in samples. Correlation coefficients (r) are between untransformed values. Significance of r at $P < 0,01$ (**). n = number of samples.

Site, Plant species	Encased larvae			r
	n	Mean numbers per plant	% of total recovered in samples	
4. *P. incana*	75	3,9	64	0,69**
5. *P. globosa*	75	10,0	56	0,62**
7. *P. globosa*	10	39,2	17	0,78**
26. *P. spinescens*	50	6,2	60	0,96**
27. *P. spinescens*	25	5,0	73	0,98**
32. *P. spinescens*	25	16,0	39	0,55**
39. *P. globosa* hybrid	25	120[1]	31	0,35
40. *P. spinescens*	15	9,2	95	-[2]

[1] Computed from the material in samples of soil beneath plant canopies (as explained in fig. 25) and the area under plant canopies. A paired t-test between this method and sifting all the soil beneath plant canopies revealed no significant difference ($P > 0,5$: 5 degrees of freedom).

[2] Too little material was outside the samples for meaningful analysis.

dom of hindsight, it may have been better to base the census on a count of the total number of *L. frustalis* encased larvae recovered from beneath the canopy of each plant. The sampling method was nevertheless quite sensitive enough to detect differences in population structure from time to time and from site to site, and certainly accurate enough to detect differences in population structure at endemic and epidemic levels of *L. frustalis*.

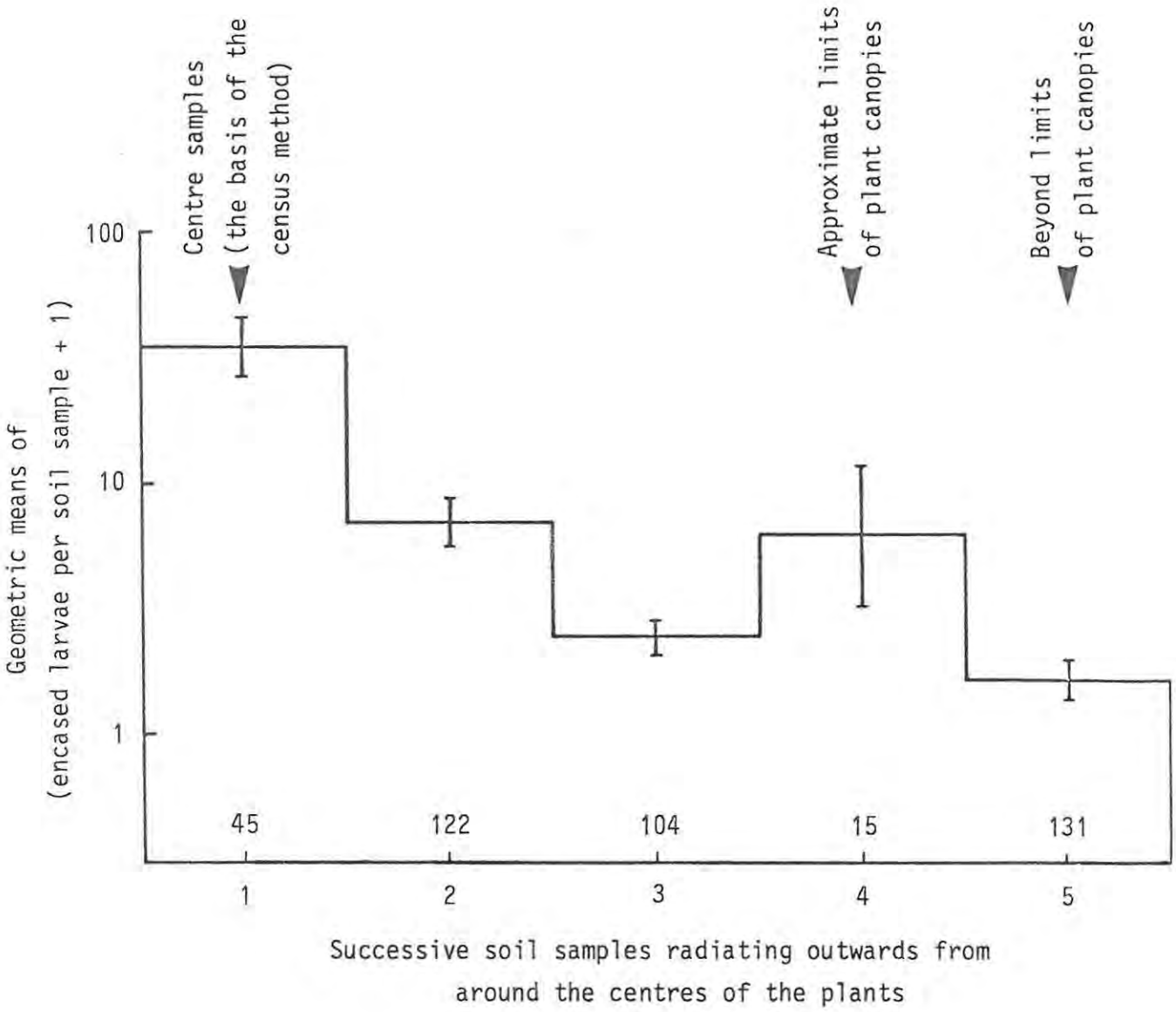


Fig. 25. The distribution of *L. frustalis* encased larvae in the soil under the canopies of *P. globosa* hybrids in Site 39. Five adjoining soil samples were taken from the centre of each plant to the periphery and replicated along 4 compass directions. Geometric means ± 95% confidence limits are shown. The numbers of samples taken in successive positions are shown above the horizontal axis.

(iii) Insect populations tend to be clumped so that counts (x) must be transformed (often to Log $(x + \frac{1}{2}k)$ where k is the dispersion parameter of the prevalent negative binomial distribution) to normalise the data (Southwood 1978). This is true for the distribution of *L. frustalis* larval cases in the soil samples.

Log (x + 1) transformations were suitable to normalise the counts for individual samples and were the only transformations used. The difficulties of balancing life tables with transformed data (Harcourt 1962; Southwood 1978; Wadley 1950) were overcome by pooling the data from individual samples for rows, a procedure which also normalised the data.

(iv) Mortalities between the 'stages' of *L. frustalis* are presented as percentages or as *k*-values, i.e. the difference between common logarithms of the numbers in successive stages (Luck 1971; Varley & Gradwell 1960, 1968). Post-larval mortality was always very low compared to the mortality for encased larvae (fig. 26) and further discussion is confined to this stage.

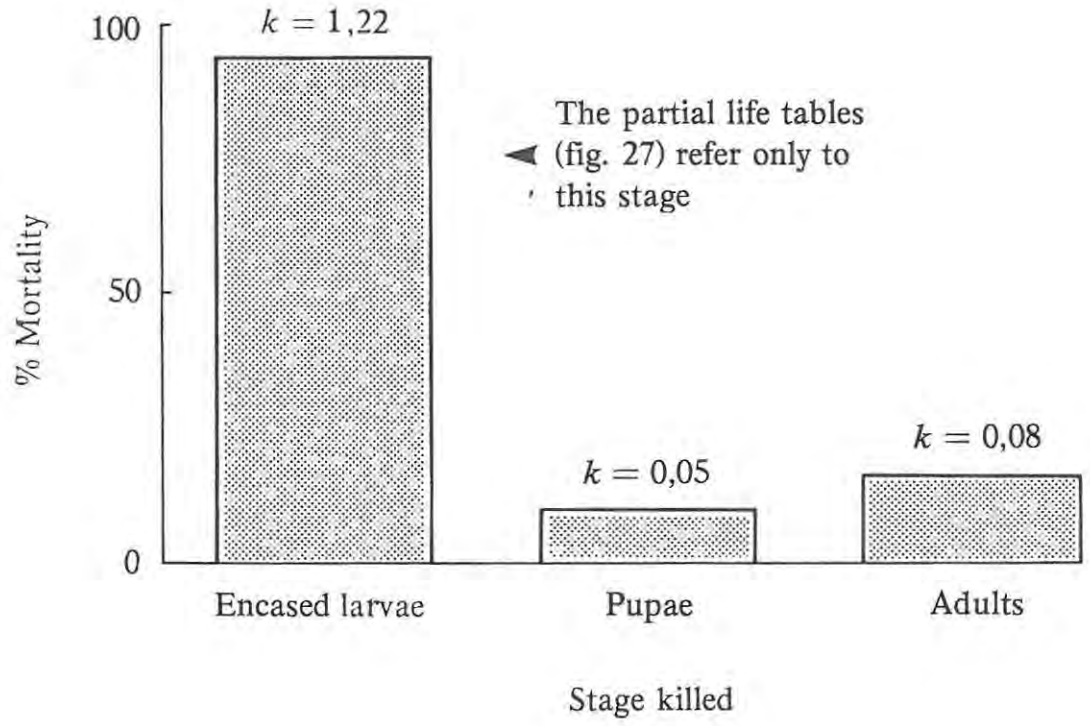


Fig. 26. The highest recorded mortalities for spent *L. frustalis* material in all census sites. Equivalent *k*-values are shown above the histogram bars.

The density of *L. frustalis* encased larvae and mortality at this stage are not statistically independent and 'proof of density dependence' was obtained in the usual way from the regressions (in common logarithms) of survivors (i.e. pupae) versus encased larvae (Smith 1973; Varley & Gradwell 1968; Varley *et al.* 1973; Watt 1964). This procedure also minimises the distortion which arises from the addition of unity (to correct for zero values), for comparisons of density relationships between individual samples. The mortality data for *L. frustalis* were analysed in terms of different densities of encased larvae in space to detect density dependence (Hassell 1980).

(v) The mortality factors which act on *L. frustalis* encased larvae are illustrated in fig. 27. The partial life tables were constructed from the main mortality factors, namely *Ch. curvimaculatus*, *M. maraisi* and *B. bassiana* (as the principal component of 'Other Mortality'), and combined 'Other Parasitoids'. Because the components of survival were predicted for dormant *L. frustalis* larvae (see (i) above) the partial life tables are similar to the end results of the population tables of Beaver (1966). For the accumulated cohorts of *L. frustalis* the partial life tables are equivalent to the sum of a number of age-specific life tables as defined by Southwood (1978). The individual mortality factors are expressed as percentage apparent mortality (Miller 1955; Morris 1957; Morris & Miller 1954).

The natural enemies of *L. frustalis* attack different stages of the host (both before and after case construction), but owing to multiple parasitism (Section 5), the data are unavoidably presented as if the natural enemies act contemporaneously (Morris 1957, 1965). The percentages can be converted to k-values -

not apportioned to the total *k*-value for the stage as done by Metcalfe (1972) for low mortalities - but without obvious benefits. Actually the discrepency, when mortalities are contemporaneous, between the sum of individual *k*-values and the total *k*-value for a stage hinders the graphical presentation of census data. In

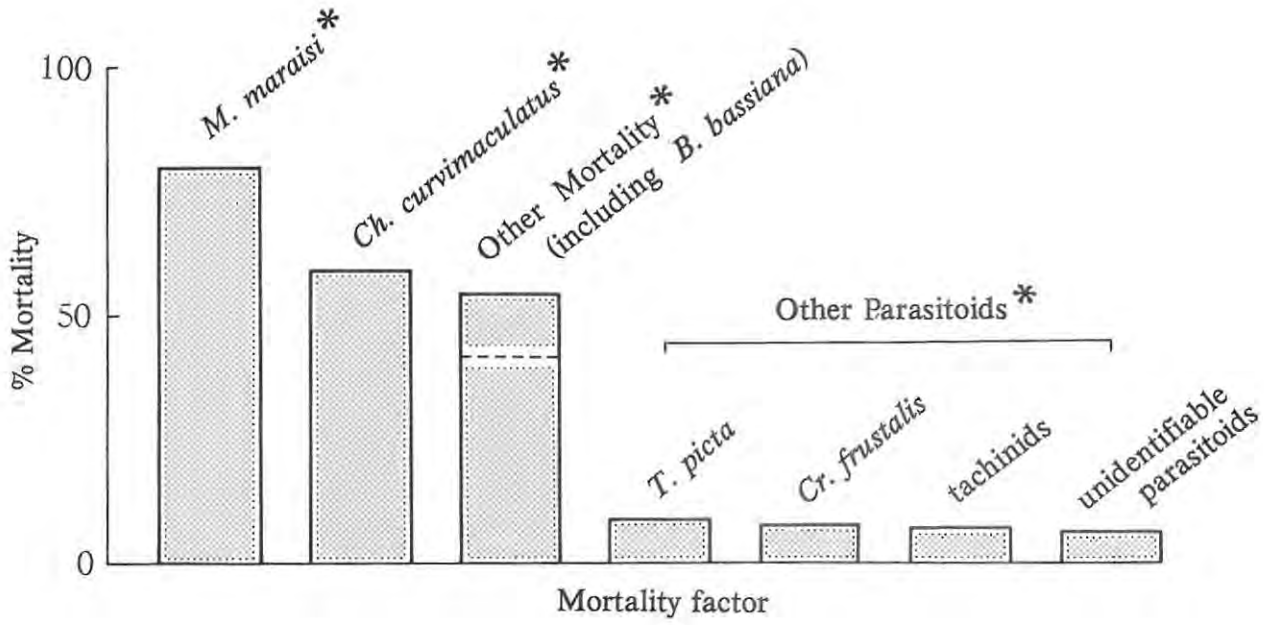


Fig. 27. The highest recorded mortalities of *L. frustalis* encased larvae in all census sites. *B. bassiana* accounts for up to 80% or more (broken line) of the 'Other Mortality' recorded in the third histogram bar, but saprophytic habits and possible secondary infections preclude a separate category for *B. bassiana*. The components of the partial life tables (Section 7) are also shown (*).

Section 7 it is shown that the assessment of individual mortality factors is plagued further by a lack of information about the mortality and dispersion of *L. frustalis* larvae before they enter the soil. In this study the 'partial life tables' are so called for want of a better term; they are not simply a part of conventional life lables as in the sense of Nebeker (1977). Ideally, the larval mortality factors should be rearranged so that encased

larvae are not regarded as a 'stage' but so that the death of fully-fed larvae is one of consecutive real mortality factors. Depending upon the nature of the earlier mortalities as discussed in Section 7, different methods for assessing mortality may be more useful.

The use of percentages, to express the contributions of individual mortality factors, highlights an important shortcoming in the census method. Because the end result of what happens in the field is recorded, the partial life tables are comprised of hosts and natural enemies which survived, so that the impact of some of the natural enemies is underestimated (through the effects of multiple parasitism) and violates part of Rule 4 (Varley *et al.* 1973: 100) for constructing budgets. Thus attempts to evaluate the regulatory impact of individual natural enemies is frustrated by assumptions that they act independently of host density and of each other.

So in summary, the census provides useful information about a critical juncture in the life history of *L. frustalis*: the numbers of encased larvae, the components of mortality and the survivors.

7. THE ABUNDANCE AND SURVIVAL OF *L. FRUSTALIS* ENCASED LARVAE

The purpose of this Section is to contrast the abundance of *L. frustalis* encased larvae and their main mortality factors in endemic and epidemic populations of the Karoo caterpillar.

THE NATURE OF LARVAL OUTBREAKS

The extent and intensity of *L. frustalis* larval outbreaks cannot be described from the census data alone. Definition is hindered by a scant knowledge of the mortality factors which act on the early stages of *L. frustalis*. Cursory field surveys of *L. frustalis* eggs during a season without significant larval outbreaks, and releases of laboratory-reared eggs in the field (including periods during which mild larval outbreaks occurred) showed that egg mortality was insignificant. This assessment includes an apparent total lack of egg parasitoids of *L. frustalis*. Nothing is known about the mortality of young *L. frustalis* larvae; the potential for mortality through catastrophies and intraspecific competition for food must, however, be high. The earliest stage of *L. frustalis* from which some information about larval outbreaks was obtained for the purpose of this study was larger larvae. These stages are conspicuous because of the damage they cause and the webs they spin around their feeding sites. Estimates indicate that 47% or less of feeding larvae eventually constructed cases in the soil. These estimates are approximate because the feeding larvae are extremely difficult to count and further, very little is known about the dispersal of larvae.

The recognition of epidemic *L. frustalis* larval outbreaks is simplified by the tendency of the larvae to be quite evenly

distributed on their pentzia hosts before the larvae begin to disperse. During outbreaks it is common for virtually every pentzia in the veld to have a conspicuous number of larvae (10 - 20 or more) feeding at the same time. A useful indicator of the severity of outbreaks, apart from the defoliation of pentzias, is the extent of larval dispersal and damage to alternate food plants of L. *frustalis*. During this study *Lycium cinereum*, species of *Rosenia* and *Walafrida saxitilis* were especially useful. There are, however, no known alternate food plants of *L. frustalis* which are always associated with pentzias and other alternate food plants are probably equally suitable in other situations.

Because *L. frustalis* larval cases accumulate in the soil, the numbers of encased larvae (which by definition include both dormant and spent material) *per se* do not allow for a differentation between endemic and epidemic outbreaks. The numbers of *L. frustalis* dormant larvae, on the other hand, provide valuable, albeit incomplete, information about the levels of outbreaks. In fig. 28 the highest numbers of dormant larvae per sample from the principle (i.e. dominant) pentzias in the census sites are shown. The figure illustrates an approximate grouping of low values for the eastern sites (Sites 4 - 25) and higher values for those in the central and western Karoo (Sites 26 - 41) - see also fig. 22 (Section 6). These data (with due regard for mortalities which occurred before censuses were conducted), together with field observations, farmers' reports of outbreaks and subsequent droughts, the information provided by the development of parasitoids (Section 5) and the freshness of *L. frustalis* larval cases, were applied to define all the populations from the eastern Karoo as endemic and all those from the central and western Karoo as epidemic.

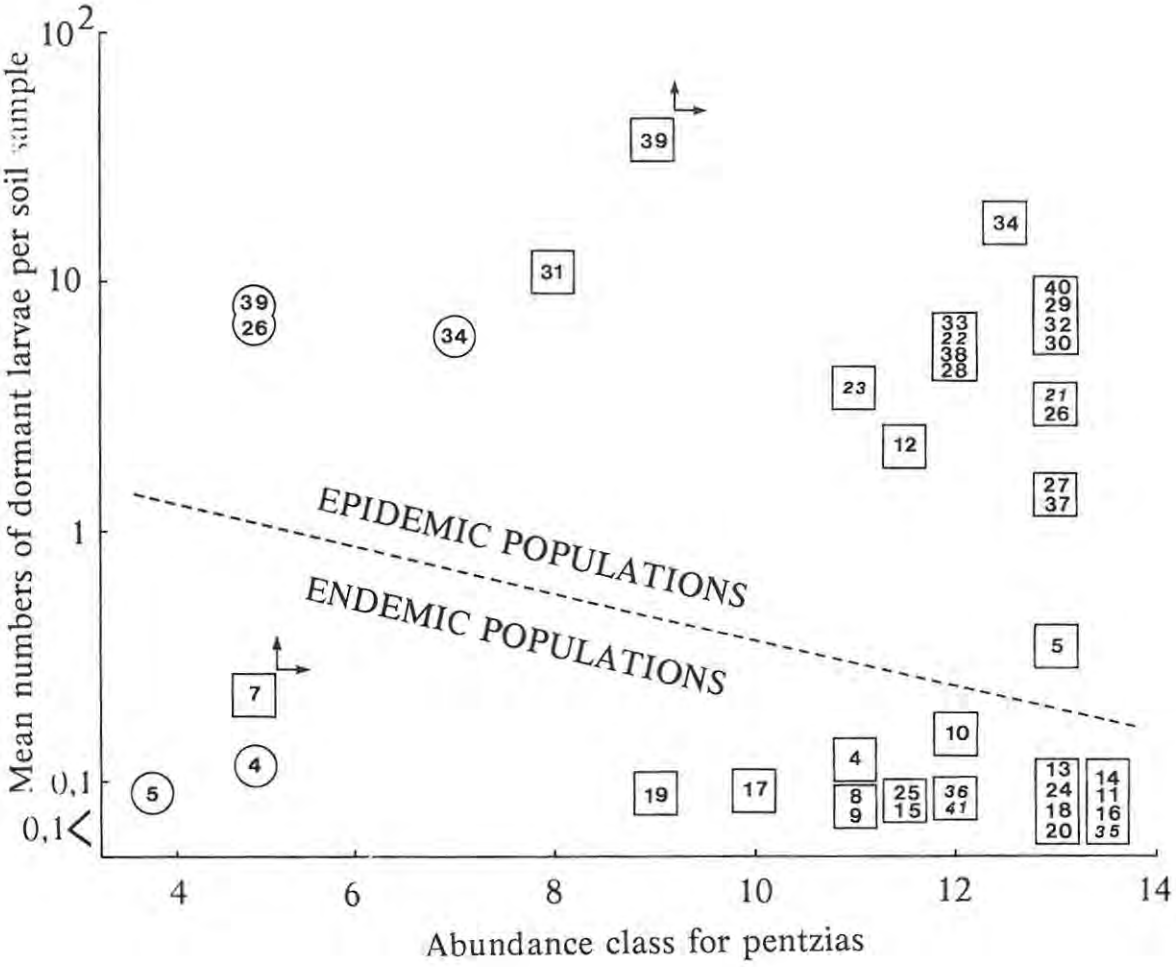


Fig. 28. The highest mean numbers of *L. frustalis* dormant larvae per soil sample collected from census sites in relation to plant abundance (Appendix 3: Table 15) for dominant pentzias (squares) and less-dominant pentzias (circles). The numbering of census sites and numbers of soil samples are shown in Table 7 (Section 6). The broken line approximately separates endemic populations (Sites 4 - 25) and epidemic populations (Sites 26 - 41): exceptions to this numbering (italicised) and the placement of Sites 1 - 3 are explained in the text. Arrows indicate underestimates of dormant larvae and plant abundance due to unusually large plant sizes.

An important additional dimension to the epidemics was their extensiveness. The recorded outbreaks were patchy in the Carnarvon area (Sites 36 - 41), more widespread in Richmond (Sites 26 - 27) and even more so in Hanover and De Aar (Sites 28 - 34). To simplify discussion this latter outbreak in the central Karoo is also called a 'pandemic'*. The pandemic outbreak was not only extensive, but particularly exciting for its intensity and spectacular dispersal of *L. frustalis* larvae. In some parts of this area pentzias, and some alternate food plants, were defoliated over virtually whole farms. Notably the generally large *L. cinereum* plants were defoliated and covered in conspicuous webs in some sites. In some areas even *Chrysocoma tenuifolia*, which has a low preference rating as food for *L. frustalis* (Appendix 3 : Table 15) was severely damaged. Interestingly, nowhere was there a complete mortality of the *L. frustalis* larvae through scramble competition for food or even an inverse relationship between damage levels and the numbers of encased larvae recovered during the subsequent censuses.

With this background it is now possible to examine host plants as determinants of *L. frustalis* abundance.

THE ROLE OF HOST PLANTS (pentzias and alternate food plants)

The nature of *L. frustalis* larval outbreaks and the sheer abundance of pentzias in the Karoo dictates that these species are the most important host plants of *L. frustalis*. This common knowledge (see references cited by Annecke & Moran (1977)) was substantiated by the results of the preliminary census of endemic

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* The term 'epidemic' includes the pandemic outbreak unless it is specified otherwise.

populations in Sites 1 - 3 (fig. 29), where the species of pentzia generally yielded more material than *Eriocephalus ericoides*, a favoured food plant of *L. frustalis* (Appendix 3 : Table 15). Forthwith it will be seen that the substantial variation in the numbers of encased larvae between the sites, especially in respect of *P. incana* (fig. 29), is of greater significance than minor differences in the palatability of food plants.

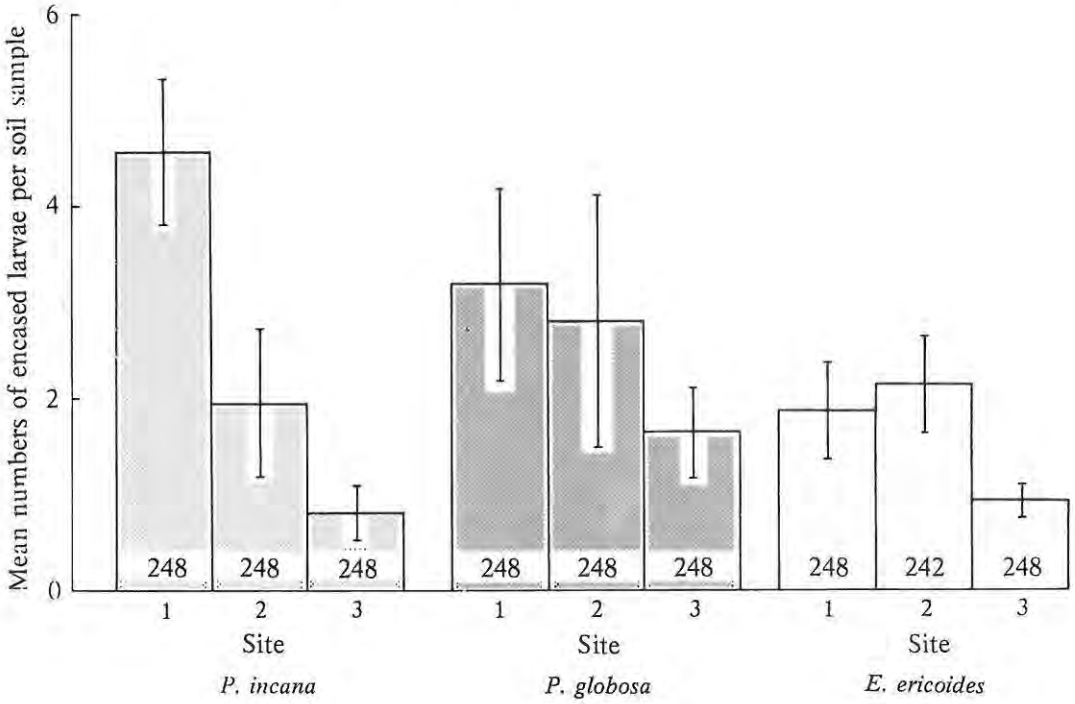

Fig. 29. The mean numbers of *L. frustalis* encased larvae per soil sample collected from 3 plant species in Sites 1 - 3. The means per sample for 11 rows ± 95% confidence limits are shown. The number of samples are shown above the horizontal axis.

WITHIN 'uniform' sites the distribution of *L. frustalis encased larvae among individual soil samples was clumped*, as already explained in Section 6. However, no general density-dependent trend (direct or inverse) was evident for the relationship between the density of encased larvae in samples and the density or abundance of host pentzias in the immediate vicinity of the sampling

points (Table 10). From these results it is clear that *encased larvae tend to be fairly evenly spread* over uniform sites; if anything, there is some evidence of a 'dilution effect', with more isolated plants being more susceptible to attack. The sites, on the other hand, are different in terms of host-plant abundance as well as vegetation type (Appendix 3 : Table 15) and a comparison of *L. frustalis* abundance BETWEEN sites follows.

The numbers of *L. frustalis* encased larvae per soil sample and the numbers per hectare (calculated from the abundance classes for pentzias approximated in Table 15 (Appendix 3)) are illustrated for the endemic populations (eastern Karoo) and for the epidemic outbreaks (central and western Karoo) in figs 30 and 31 respectively. These figures show that on the basis of *L. frustalis* encased larvae per sample there is no marked increase in numbers as pentzias become more abundant (but see Discussion for an example of variability between contrasting sites), but that the number of encased larvae per hectare increases as a function of the abundance of pentzias. So when the census data are related to the abundance of pentzias and expressed as the numbers of *L. frustalis* per hectare, as in the upper sets of data in figs 30 and 31, differences caused by the abundance of host plants are accentuated by the logarithmic increase in the numbers of plants in successive abundance classes (Appendix 3 : fig. 40). The relative contributions of dominant and less-dominant species of *Pentzia* (indicated as circles in the figures) to *L. frustalis* abundance at any one site are particularly striking. However the census data are viewed, given the knowledge about the even distribution of *L. frustalis* in sites and the near-total defoliation which sometimes occurs, the densest patches of pentzias always

Table 10. The numbers of *L. fruticum* encased larvae per soil sample in relation to to the abundance classes of pentzias in 100 m² plots (Appendix 3 : Table 15) and the density of pentzias (estimated by distance measurements - see Section 3). *n* = number of soil samples. Zero values were distributed independently of host-plant abundance and density, and are excluded from the regression equations. Significance tests are based on 2 standard errors and are approximated by values of *r* ($P < 0,05$).

Site, Plant species	*n*	Mean numbers of encased larvae per soil sample	*r*	Density relationship
ABUNDANCE				
4. *P. incana*	45	Log (y + 1) = 0,004x + 0,50	0,03	Independent
5. *P. globosa*	58	Log (Y + 1) = 0,03x + 0,32	0,14	Independent
8. *P. globosa*	10	Log (y + 1) = 0,01x + 0,26	0,09	Independent
9. *P. globosa*	21	Log (y + 1) = -0,01x + 0,56	0,16	Independent
8 - 9. *P. globosa*	32	Log (y + 1) = -0,01x + 0,49	0,10	Independent
13, 17 - 20. *P. globosa*	41	Log (y + 1) = 0,01x + 0,40	0,05	Independent
21. *P. incana*	23	Log (y + 1) = -0,06x + 1,64	0,26	Independent
22. *P. incana*	23	Log (y + 1) = -0,03x + 1,32	0,12	Independent
26. *P. spinescens*	164	Log (y + 1) = -0,04x + 1,22	0,20	Independent
27. *P. spinescens*	96	Log (y + 1) = -0,09x + 1,68	0,24	Inverse
32. *P. spinescens*	35	Log (y + 1) = 0,05x + 0,16	0,16	Independent
39. *P. globosa* hybrid	24	Log (y + 1) = 0,06x + 0,93	0,13	Independent
40. *P. spinescens*	70	Log (y + 1) = 0,01x + 0,54	0,06	Independent
DENSITY				
4. *P. incana*	39	Log (y + 1) = $-0,12x^{0,5}$ + 0,85	0,41	Inverse
5. *P. globosa*	66	Log (y + 1) = $0,04x^{0,5}$ + 0,83	0,06	Independent
26. *P. spinescens*	17	Log (y + 1) = $0,08x^{0,5}$ + 0,61	0,09	Independent
39. *P. globosa* hybrid	25	Log (y + 1) = $-0,27x^{0,5}$ + 1,89	0,19	Independent
40. *P. spinescens*	72	Log (y + 1) = $0,03x^{0,5}$ + 0,91	0,07	Independent

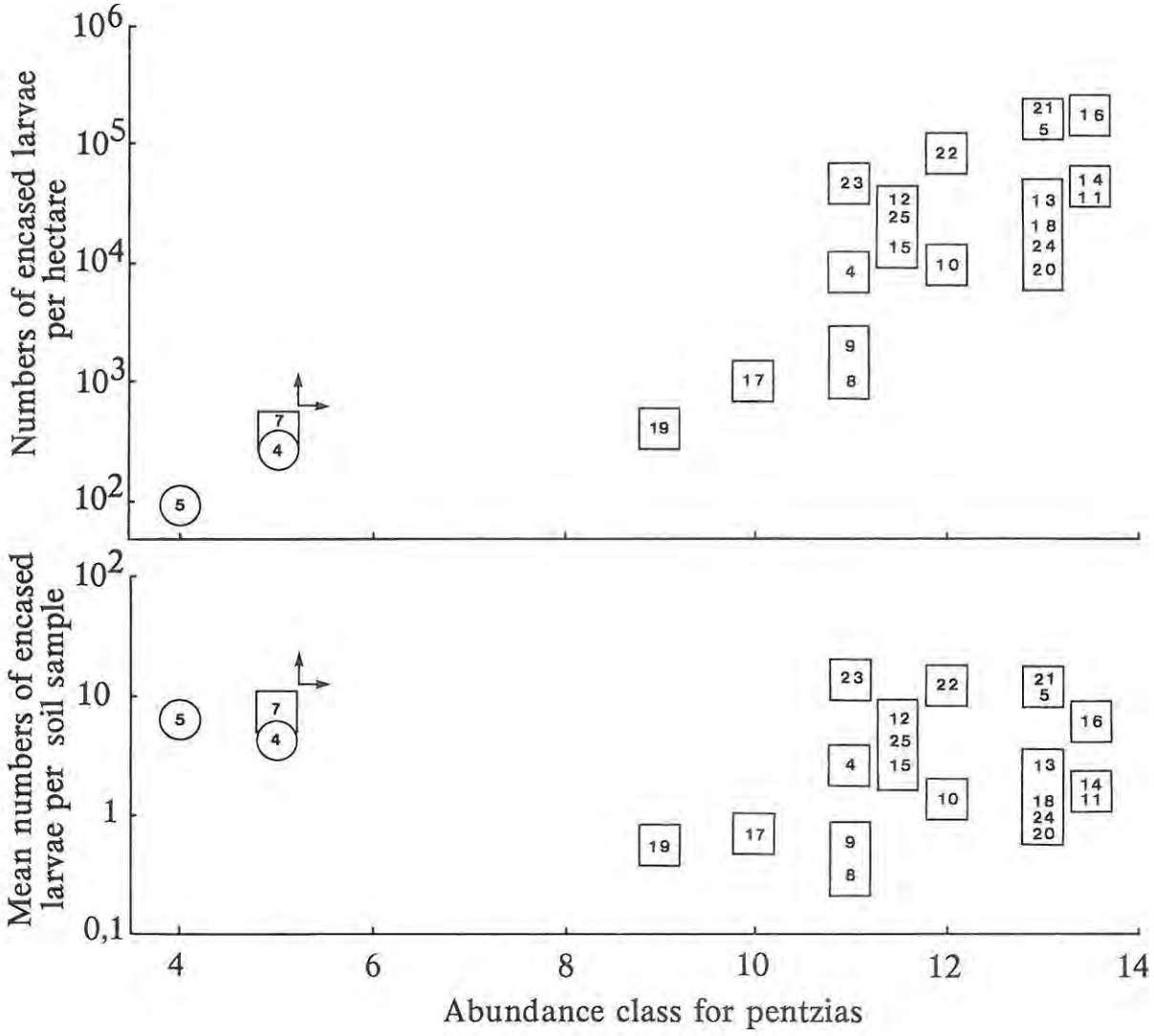

Fig. 30. The mean numbers of *L. frustalis* encased larvae per soil sample and the total per hectare (see text) in relation to plant abundance (Appendix 3: Table 15) for dominant pentzias (squares) and less-dominant pentzias (circles) in the endemic populations of the eastern Karoo. The numbering of census sites and the numbers of soil samples are shown in Table 7 (Section 6) and Table 13 (which also shows the raw data). Arrows indicate underestimates of 'per plant' values and plant abundance due to unusually large plant sizes.

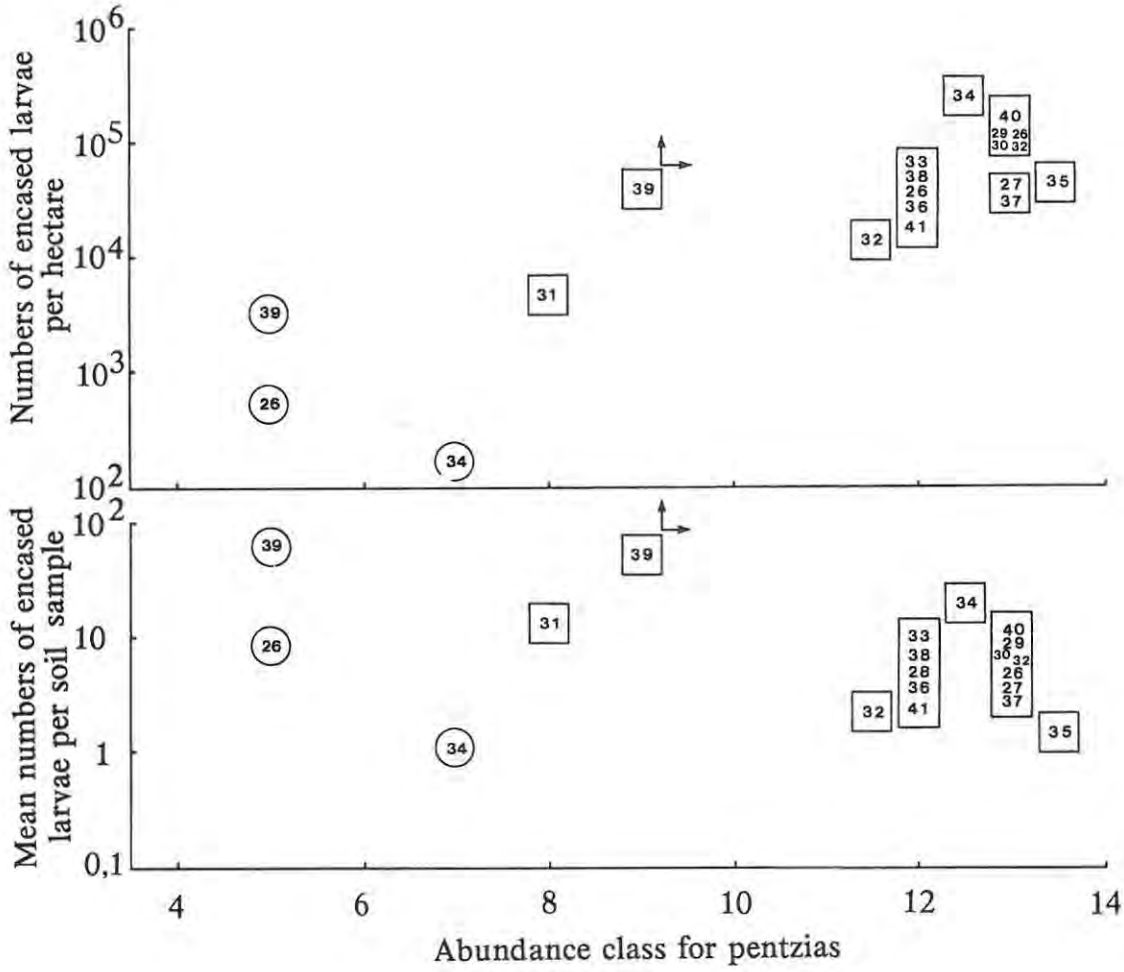

Fig. 31. The mean numbers of *L. frustalis* encased larvae per soil sample and the total per hectare (see text) in relation to plant abundance (Appendix 3: Table 15) for dominant pentzias (squares) and less-dominant pentzias (circles) in the epidemic populations of the central and western Karoo. The numbering of census sites and the numbers of soil samples are shown in Table 7 (Section 6) and Table 13 (which also shows the raw data). Arrows indicate under-estimates of 'per plant' values and plant abundance due to unusually large plant sizes. Duplicated values for Site 32 are due to sub-plots.

produce most encased larvae of the Karoo caterpillar.

Alternate food plants of *L. frustalis* are significant during epidemic outbreaks when they are reached by dispersing *L. frustalis* larvae. The census data do not provide an assessment of the susceptibility of the vegetation in the various sites - too few plant species have been screened for suitability to *L. frustalis* (Appendix 3: Table 15) and moreover, the extent to which alternate food plants are attacked depend upon the abundance of *L. frustalis* and the community structure of the vegetation. This is illustrated for some plant species within sites in fig. 32.

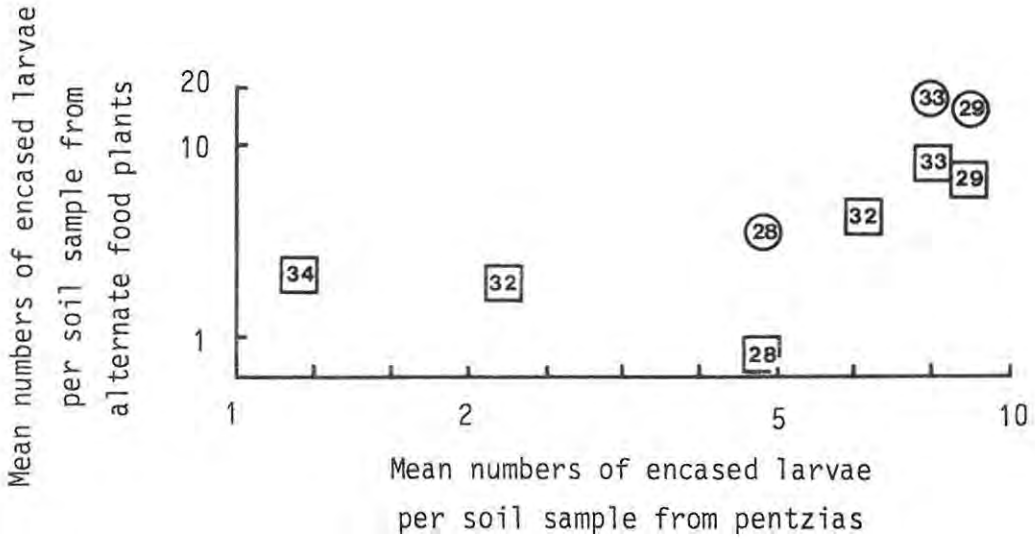

Fig. 32. The mean numbers of *L. frustalis* encased larvae per soil sample collected from alternate food plants in relation to the numbers collected from nearby pentzias (Appendix 3: Table 15) in the same census sites. The numbering of census sites and the numbers of soil samples are shown in Table 7 (Section 6) and Table 13 (which also shows the raw data). The alternate food plants are *Rosenia humilis* (circles) and *Walafrida saxitilis* (squares). Duplicated values for Site 32 are due to sub-plots. Site 34 represents the less-dominant *P. spinescens*.

In Table 11 the numbers of *L. frustalis* encased larvae from pentzias and some alternate food plants are recorded. Immediately apparent from the per sample values (Table 11) is the potential of some alternate food plants to increase the numbers of *L. frustalis* which eventually construct cases. In some of the sites, more material was recovered from alternate food plants than from pentzia itself. Alternate food plants are sometimes very abundant and an indication of their yield of *L. frustalis* per hectare is also shown in Table 11. These data are imprecise because the census method was developed with a view to sampling pentzias; some values for generally large species are obviously underestimates and are identified in the table.

The alternate food plants separate into two categories, those on which all the larval stages of *L. frustalis* are able to feed and complete their development, and others on which only slight feeding is possible but which in some situations allow large numbers of *L. frustalis* larvae to complete their feeding and survive. Notable examples of plants with a relatively low rating as food for the Karoo caterpillar (Appendix 3: Table 15), but from which many encased larvae were collected (Table 11), or seen to be fed on in the field, include species of *Pteronia* and *Salsola*, *Plinthus karooicus* and *Chrysocoma tenuifolia*. The significance of palatable alternate food plants and non-host plants of *L. frustalis* is dealt with in the Discussion in the context of the pest status of *L. frustalis* and the ecological status of some Karoo plants.

The number of *L. frustalis* encased larvae in the soil does not necessarily reflect the number of survivors. This depends at least partly upon their natural enemies.

Table 11. The numbers of *L. frustalis* encased larvae per soil sample and the total per hectare (see text) collected from under pentzia host plants and alternate food plants for the epidemic populations of the central and western Karoo. *n* = number of soil samples. Underestimates (*) of 'per plant' values and plant abundance are due to unusually large plant sizes. Host-plant status is as recorded in Table 15 (Appendix 3) - the terminology is explained in Section 3.

Site, Plant species	*n*	Host-plant status	Numbers of encased larvae	
			Per soil sample	Per hectare (X 1 000)
26. *C. tenuifolia*	75	Low	0,8	0,2
P. incana	25	Host plant	9	0,5
P. spinescens	600	Host plant	5	69
28. *P. globosa*	150	Host plant	5	36
R. humilis	25	High	3	1
W. saxitilis	25	High	0,8	5
29. *P. globosa*	25	Host plant	9	134
M. karooicus	10	Negligible	4	5
R. humilis	25	High	16	5
W. saxitilis	25	High	7	8
30. *E. ericoides**	10	High	12	4
P. spinescens	50	Host plant	7	108
*Pt. glauca**	10	Low	4	0,2
31. *P. globosa*	10	Host plant	13	5
S. calluna	10	Intermediate	11	3
*Z. incrustatum**	10	High	22	27
32. *P. spinescens*	125	Host plant	5	36
W. saxitilis	50	High	3	0,9
33. *P. globosa*	25	Host plant	8	60
R. humilis	25	High	17	5
W. saxitilis	25	High	8	2
34. *P. globosa*	10	Host plant	20	250
P. spinescens	25	Host plant	1	0,4
W. saxitilis	25	High	2	0,6
39. *Chrysocoma* spp.	60	Low	14	17
P. globosa hybrid*	200	Host plant	51	39
P. incana	15	Host plant	64	4

THE ROLE OF NATURAL ENEMIES

This section is mainly about the total mortality of *L. frustalis* encased larvae caused by the collective action of natural enemies and other mortality factors in endemic and epidemic populations. Within-site and between-site relationships are described in order to weigh the impact of natural enemies on *L. frustalis* populations against the role of host plants as determinants of *L. frustalis* abundance. Lastly, the contributions of individual natural enemies are presented.

WITHIN-SITE relationships between mortality and the density of *L. frustalis* encased larvae in individual soil samples are shown in Table 12 for many areas and several plant species. For the endemic populations (Sites 4 - 25) the density relationships were direct for nearly 80% of the tabulated interactions and no density relationship could be established for the remainder of the endemic populations. Similar results were obtained for the epidemic populations (Sites 26 - 41), but with the exception of the Hanover - De Aar pandemic outbreak (Sites 28 - 34). The results for these latter sites are inconclusive due to shortcomings in the method of analysis (see Section 6 : fig 23, Footnote 8), the exceptionally low rates of parasitism in some of these sites (below) and the unexplained effects of larval dispersal known to have occurred. In none of the sites was there any evidence of an inverse density-dependent relationship. In all, the general trend of undercompensating direct density-dependent responses by the natural enemies to the patchy distribution of *L. frustalis* between host plants, is significant and in keeping with a large body of theoretical and empirical evidence (see for example Hassell 1980; Holling 1961; Stubbs 1977; Waage 1979).

Table 12. The relationship between mortality and the density of *L. frustalis* encased larvae per sample. Significance tests are based on the survivors per sample (see Section 6) and are approximated by values of r ($P < 0,05$). The higher case applies to dominant pentzias in sites. Endemic and epidemic populations are defined in the text. n = number of soil samples (note that n does not necessarily correspond to n tabulated elsewhere.

	Site, Plant species	n	k-value	Density relationship	r
ENDEMIC POPULATIONS	MIDDELBURG				
	4. *Pentzia* spp.	150	y = 0,54 Log (x + 1) + 0,07	Direct	0,64
	P. globosa	75	y = 0,55 Log (x + 1) + 0,10	Direct	0,60
	P. INCANA	75	y = 0,43 Log (x + 1) + 0,17	Direct	0,56
	5. *L. cinereum*	25	y = 0,30 Log (x + 1) + 0,17	Direct	0,50
	Pentzia spp.	150	y = 0,31 Log (x + 1) + 0,16	Direct	0,53
	P. GLOBOSA	75	y = 0,27 Log (x + 1) + 0,12	Direct	0,43
	P. incana	75	y = 0,35 Log (x + 1) + 0,14	Direct	0,56
	R. humilis	10	y = 0,06 Log (x + 1) + 0,25	Independent	0,20
	S. calluna	40	y = 0,37 Log (x + 1) + 0,08	Direct	0,57
	4 - 5. *Pentzia* spp.	150	y = 0,27 Log (x + 1) + 0,18	Direct	0,41
	6. *E. ericoides*	75	y = 0,35 Log (x + 1) + 0,07	Direct	0,51
	7. *P. GLOBOSA*	20	y = 0,05 Log (x + 1) + 0,33	Independent	0,08
	8. *P. GLOBOSA*	75	y = 0,29 Log (x + 1) + 0,09	Independent	0,31
	9. *P. GLOBOSA*	75	y = 0,45 Log (x + 1) + 0,08	Direct	0,42
	8 - 9. *P. globosa*	150	y = 0,42 Log (x + 1) + 0,07	Direct	0,41
	10. *P. GLOBOSA*	25	y = 0,65 Log (x + 1) + 0,07	Direct	0,65
	11. *P. GLOBOSA*	10	y = 0,16 Log (x + 1) + 0,30	Independent	0,15
	10 - 11. *P. GLOBOSA*	35	y = 0,57 Log (x + 1) + 0,10	Direct	0,57
	12. *P. GLOBOSA*	10	y = 0,87 Log (x + 1) - 0,06	Direct	0,85
	13. *P. GLOBOSA*	35	y = 0,68 Log (x + 1) - 0,03	Direct	0,57
	14. *P. GLOBOSA*	10	y = 1,05 Log (x + 1) - 0,09	Direct	0,91
	15. *P. GLOBOSA*	10	y = 0,69 Log (x + 1) + 0,11	Direct	0,81
	16. *P. GLOBOSA*	10	y = 0,37 Log (x + 1) + 0,21	Direct	0,61
	17. *P. GLOBOSA*	10	y = 1,19 Log (x + 1) - 0,14	Direct	0,76
	18. *P. GLOBOSA*	25	y = 0,57 Log (x + 1) + 0,00	Direct	0,57
	19. *P. GLOBOSA*	25	y = 0,74 Log (x + 1) - 0,08	Direct	0,88
	20. *P. GLOBOSA*	25	y = 0,28 Log (x + 1) + 0,18	Independent	0,28
	10 - 20. *P. GLOBOSA*	210	y = 0,68 Log (x + 1) + 0,03	Direct	0,71
	21. *P. INCANA*	25	y = 0,08 Log (x + 1) + 0,39	Independent	0,11
	22. *P. INCANA*	25	y = 0,35 Log (x + 1) + 0,09	Independent	0,37
	23. *P. INCANA*	25	y = 0,56 Log (x + 1) - 0,07	Direct	0,64
	21 - 23. *P. INCANA*	75	y = 0,37 Log (x + 1) + 0,09	Direct	0,44
	CRADOCK				
	24. *P. INCANA*	75	y = 0,68 Log (x + 1) + 0,06	Direct	0,70
	ADELAIDE				
	25. *P. INCANA*	35	y = 0,35 Log (x + 1) + 0,07	Direct	0,45
EPIDEMIC POPULATIONS	RICHMOND				
	26. *P. incana*	25	y = 0,35 Log (x + 1) - 0,10	Direct	0,51
	P. SPINESCENS	75	y = 0,24 Log (x + 1) + 0,07	Direct	0,39
	27. *P. SPINESCENS*	75	y = 0,24 Log (x + 1) + 0,06	Direct	0,34
	26 - 27. *Pentzia* spp.	191	y = 0,23 Log (x + 1) + 0,06	Direct	0,40
	HANOVER				
	28. *P. GLOBOSA*	75	y = -0,27 Log (x + 1) + 0,15	Independent	0,15
	R. humilis	25	y = -0,05 Log (x + 1) + 0,12	Independent	0,13
	29. *P. GLOBOSA*	25	y = -0,26 Log (x + 1) + 0,60	Independent	0,34
	R. humilis	25	y = 0,19 Log (x + 1) - 0,06	Independent	0,25
	W. saxitilis	25	y = 0,06 Log (x + 1) + 0,14	Independent	0,10
	DE AAR				
	30. *E. ericoides*	10	y = 0,03 Log (x + 1) + 0,06	Independent	0,06
	P. SPINESCENS	25	y = 0,22 Log (x + 1) + 0,07	Independent	0,33
	Pt. glauca	10	y = 0,40 Log (x + 1) + 0,19	Direct	0,61
	31. *P. GLOBOSA*	10	y = 0,11 Log (x + 1) + 0,14	Independent	0,22
	S. calluna	10	y = -0,14 Log (x + 1) + 0,28	Independent	0,29
	Z. incrustatum	10	y = -0,11 Log (x + 1) + 0,34	Independent	0,31
	32. *P. SPINESCENS*	100	y = 0,08 Log (x + 1) + 0,08	Independent	0,15
	W. saxitilis	50	y = 0,31 Log (x + 1) - 0,04	Direct	0,39
	33. *P. GLOBOSA*	25	y = -0,09 Log (x + 1) + 0,29	Independent	0,17
	R. humilis	25	y = 0,04 Log (x + 1) + 0,09	Independent	0,08
	W. saxitilis	25	y = -0,01 Log (x + 1) + 0,26	Independent	0,01
	34. *P. GLOBOSA*	10	y = 0,79 Log (x + 1) - 0,38	Direct	0,55
	P. spinescens	25	y = 0,07 Log (x + 1) + 0,02	Direct	0,94
	W. saxitilis	25	y = 0,22 Log (x + 1) + 0,03	Independent	0,40
	30 - 34. *Pentzia* spp.	195	y = 0,23 Log (x + 1) + 0,02	Direct	0,35
	VICTORIA WEST				
	35. *P. SPINESCENS*	25	y = 0,59 Log (x + 1) + 0,00	Direct	0,48
	CARNARVON				
	36. *P. SPINESCENS*	50	y = 0,05 Log (x + 1) + 0,22	Independent	0,09
	37. *P. SPINESCENS*	75	y = 0,40 Log (x + 1) + 0,18	Direct	0,59
	38. *P. SPINESCENS*	50	y = 0,33 Log (x + 1) - 0,02	Direct	0,53
	39. *Chrysocoma* spp.	60	y = 0,54 Log (x + 1) + 0,04	Direct	0,70
	P. GLOBOSA hybrid	100	y = 0,60 Log (x + 1) + 0,06	Direct	0,58
	P. incana	15	y = -0,02 Log (x + 1) + 0,89	Independent	0,01
	40. *P. SPINESCENS*	75	y = 0,33 Log (x + 1) + 0,07	Direct	0,37
	41. *P. SPINESCENS*	25	y = 0,25 Log (x + 1) + 0,04	Independent	0,36

At endemic population levels the density relationships between samples were clearly of greater significance than the relationship between mortality and the mean density per sample of *L. frustalis* encased larvae BETWEEN SITES shown in Table 13. Between comparable sites in the eastern Karoo (Sites 1 - 25) identified in Table 13, mortality rates varied only slightly and were, therefore, independent of the corresponding variation in the density of encased larvae. For the epidemic populations of the central and western Karoo (Sites 26 - 41), on the other hand, the mortality of the encased larvae was directly related to their density (Table 13, fig. 33). The three pie-diagrams (fig. 34) derived from the data in Table 13 emphasize the essential differences between the mortality in the endemic, epidemic and pandemic populations. Mortality was greatest in the endemic populations, less so in the epidemics and least of all in the pandemics.

A further point needs emphasis. It has already been shown that the numbers of *L. frustalis* encased larvae recorded per hectare was related to the abundance of pentzias for endemic and epidemic populations (figs 30 - 31). This relationship was maintained in populations of *L. frustalis* encased larvae that had survived natural-enemy induced mortality (figs 35 - 36). Clearly, the density-dependent responses of *L. frustalis* natural enemies that have just been discussed were unable to override or compensate for the powerful influence of host-plant density on *L. frustalis* populations.

Alternate food plants of *L. frustalis* also have profound effects on the *L. frustalis* natural enemies. Although the density relationship between encased larvae and their survival on alternate food plants was similar to that on the pentzias and tended

Table 13. Partial life tables for *H. frustalis* encased larvae. The mortality factors are *Ch. curvimaculatus* (C), *M. araisi* (M), Other Parasitoids (P) and Other Mortality (O). The higher case applies to dominant pentzias in sites. Endemic and epidemic populations are defined in the text. *n* = number of soil samples.

	Site, Plant species	*n*	Mean numbers of encased larvae per soil sample	Mortality factors (%) C	M	P	O	Total mortality (%)
ENDEMIC POPULATIONS	MIDDELBURG							
1 - 3.	*E. ericoides*	738	1,53	6	43	4	8	61
	P. globosa	744	2,32	6	44	4	14	68
	P. incana	744	2,32	6	44	4	8	62
4.	*P. globosa*	75	4,64	7	34	7	35	83
	P. INCANA	525	2,66	4	42	7	25	78
5.	*G. procumbens*	75	0,00	-	-	-	-	-
	L. cinereum	25	2,36	5	49	5	14	73
	P. GLOBOSA	525	9,45	9	32	11	22	74
	P. incana	75	6,45	8	47	6	12	73
	R. humilis	10	4,10	5	29	2	22	58
	S. calluna	40	5,30	3	49	8	9	69
6.	*E. ericoides*	375	2,13	5	44	9	5	63
7.	*P. GLOBOSA*	20	7,00	5	34	11	9	59
8.	*P. GLOBOSA*	75	0,29	9	36	4	14	63
9.	*C. tenuifolia*	75	0,01	-	-	-	-	-
	P. GLOBOSA	75	0,60	2	27	9	29	67
10.	*P. GLOBOSA*	25	1,36	6	32	6	41	85
11.	*P. GLOBOSA*	10	1,50	7	20	0	53	80
12.	*P. GLOBOSA*	10	6,10	16	20	8	46	90
13.	*P. GLOBOSA*	35	2,24	0	13	2	50	65
14.	*P. GLOBOSA*	10	1,60	13	31	0	50	94
15.	*P. GLOBOSA*	10	2,60	12	27	8	46	93
16.	*P. GLOBOSA*	10	6,00	12	37	7	27	83
17.	*P. GLOBOSA*	25	0,68	6	71	6	6	89
18.	*P. GLOBOSA*	25	1,12	4	32	7	25	68
19.	*P. GLOBOSA*	25	0,56	0	79	0	0	79
20.	*P. GLOBOSA*	25	0,64	6	13	6	50	75
	W. saxitilis	25	0,00	-	-	-	-	-
21.	*P. INCANA*	50	14,16	7	27	6	26	66
22.	*P. INCANA*	50	12,30	2	25	6	31	64
23.	*P. INCANA*	50	14,28	6	28	6	17	57
	CRADOCK							
24.	*P. INCANA*	105	1,11	11	59	9	7	86
	ADELAIDE							
25.	*P. INCANA*	35	4,86	10	29	4	19	62
EPIDEMIC POPULATIONS	RICHMOND							
26.	*C. tenuifolia*	75	0,76	0	9	7	4	20
	P. incana	25	9,44	20	9	5	15	49
	P. SPINESCENS	600	4,62	14	17	5	15	51
27.	*P. SPINESCENS*	150	2,79	17	23	3	10	53
	HANOVER							
28.	*P. GLOBOSA*	150	4,82	3	5	1	10	19
	R. humilis	25	3,36	1	5	0	8	14
	W. saxitilis	25	0,80	0	0	0	5	5
29.	*P. GLOBOSA*	25	8,96	27	12	1	11	51
	Pl. karooicus	10	3,70	13	0	0	6	19
	R. humilis	25	15,50	12	4	1	12	29
	W. saxitilis	25	6,54	20	5	1	6	32
	DE AAR							
30.	*E. ericoides*	10	11,90	4	11	2	4	21
	P. SPINESCENS	50	7,18	19	18	1	17	55
	Pt. glauca	25	3,64	33	11	1	28	73
31.	*P. GLOBOSA*	10	12,95	11	5	0	29	45
	S. calluna	10	11,10	0	1	0	12	13
	Z. incrustatum	10	21,60	9	6	1	19	35
32.	*P. SPINESCENS*	125	4,84	10	10	1	10	31
	W. saxitilis	50	2,96	16	4	1	11	32
33.	*P. GLOBOSA*	25	7,96	17	3	1	15	36
	R. humulis	25	16,77	8	4	0	13	25
	W. saxitilis	25	8,27	16	2	0	11	29
34.	*P. GLOBOSA*	10	19,96	57	10	1	10	78
	P. spinescens	25	1,20	7	0	0	12	19
	W. saxitilis	25	2,08	15	8	0	4	27
	VICTORIA WEST							
35.	*P. SPINESCENS*	25	1,44	25	17	0	25	67
	CARNARVON							
36.	*P. SPINESCENS*	50	4,50	17	12	14	7	50
37.	*P. SPINESCENS*	150	2,75	24	37	9	8	78
38.	*P. SPINESCENS*	60	6,70	7	22	4	24	57
39.	*Chrysocoma* spp.	60	13,66	29	16	6	30	81
	P. GLOBOSA hybrid	200	51,39	22	26	9	35	92
	P. incana	15	64,49	18	18	8	39	83
40.	*P. SPINESCENS*	225	10,83	10	39	5	9	63
41.	*P. SPINESCENS*	25	2,32	9	24	7	5	45

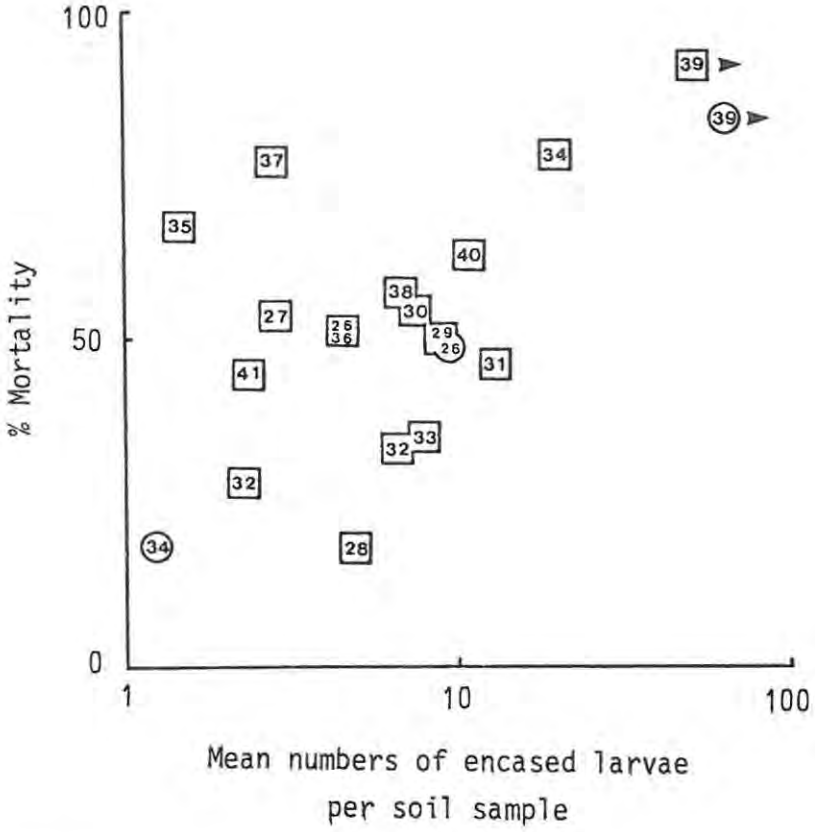

Fig. 33. The relationship between the % mortality and mean numbers of *L. frustalis* encased larvae per soil sample for dominant pentzias (squares) and less-dominant pentzias (circles) in the epidemic populations of the central and western Karoo. The numbering of census sites and the numbers of soil samples are shown in Table 7 (Section 6) and Table 13 (which also shows the raw data). Arrows indicate underestimates of 'per plant' values and plant abundance due to unusually large plant sizes. Duplicated values for Site 32 are due to sub-plots.

towards undercompensating direct density dependence (Table 12), the mortality rates for sites were mostly lower since all the natural enemies were generally scarcer when associated with alternate food plants (fig. 37) than the pentzias (fig. 34). These reduced mortality rates served to increase the already-significant contributions of alternate food plants to *L. frustalis* abundance previously discussed (Table 11).

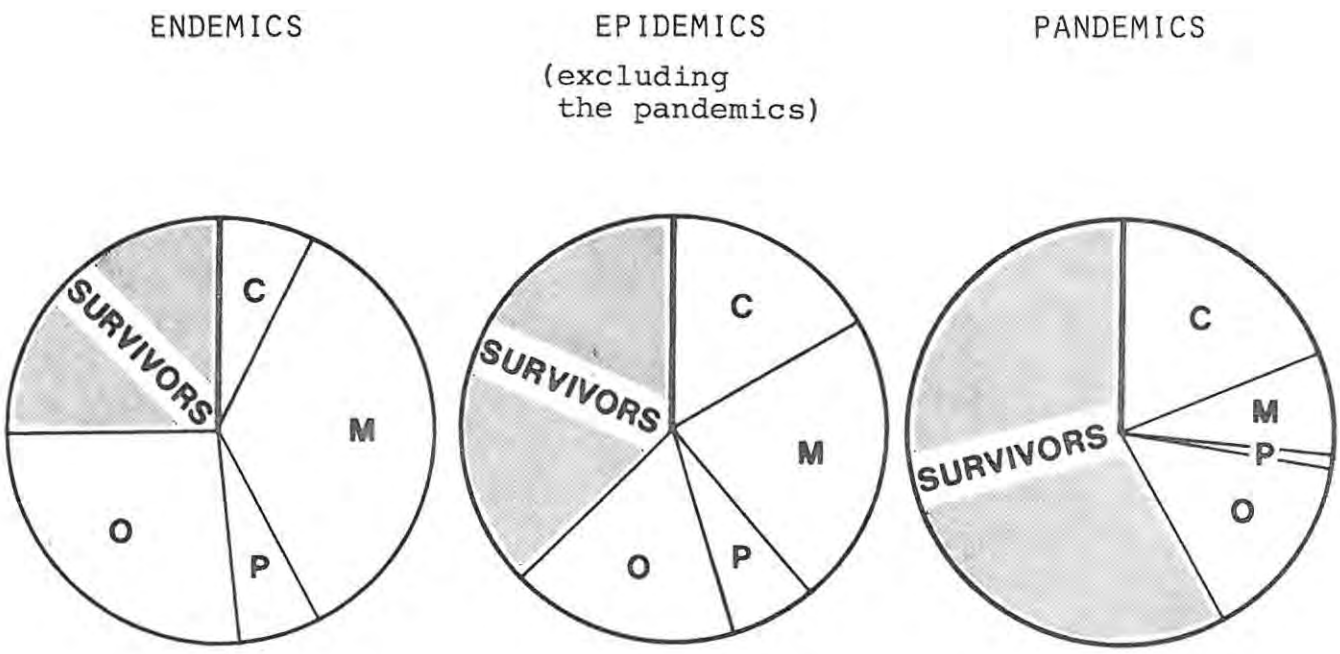

Fig. 34. The proportions of surviving and killed *L. frustalis* encased larvae collected from the soil under pentzias for the endemic populations of the eastern Karoo (Sites 1 - 25), epidemic populations of the central and western Karoo (Sites 26 - 27 and 35 - 41) and pandemic populations (Sites 28 -34). The mortality factors are *Ch. curvimaculatus* (C), *M. maraisi* (M), Other Parasitoids (P) and Other Mortality (O). The diagrams are derived from the data in Table 13.

The method of analysing the census data does not provide precise estimates of the roles of individual natural enemies of *L. frustalis*. Marked differences between them do, however, emerge when the data are viewed on a regional basis. *M. maraisi* is clearly the most widespread parasitoid, particularly for endemic populations (fig. 34). *Ch. curvimaculatus*, however, has been underrated in this and previous studies. The high rates of parasitism by *Ch. curvimaculatus* in some of the epidemics (fig. 34) are of special significance - the *L. frustalis* egg populations must have been enormous - for they give a clear indication of a direct

response to host density. This parasitoid is exposed to multiple parasitism longer than the others - virtually all its life - and generally is killed by the other parasitoids of *L. frustalis* (Section 5 : fig. 19). Calculations of parasitism from the proportions of fourth-instar *L. frustalis* encased larvae from some of the sites revealed that underestimates of parasitism by *Ch.*

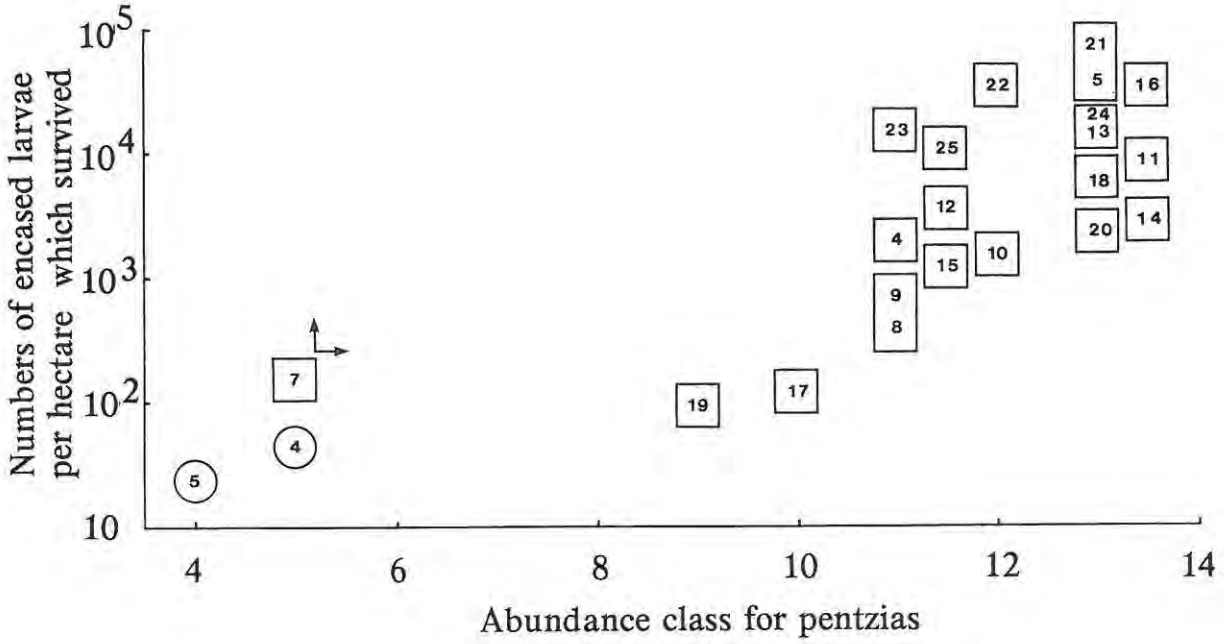

Fig. 35. The total numbers of *L. frustalis* encased larvae per hectare (see text) which survived in relation to plant abundance (Appendix 3 : Table 15) for dominant pentzias (squares) and less-dominant pentzias (circles) in the endemic populations of the eastern Karoo. The numbering of census sites, the numbers of soil samples and the raw data are shown in Table 13. Arrows indicate underestimates of encased larvae and plant abundance due to unusually large plant sizes.

curvimaculatus of 10 - 20 % were quite common. The low rates of parasitism of *L. frustalis* by Other Parasitoids (Table 13) may be misleading - Morris (1965) illustrates that low mortalities acting contemporaneously with others are easily underrated. Of the

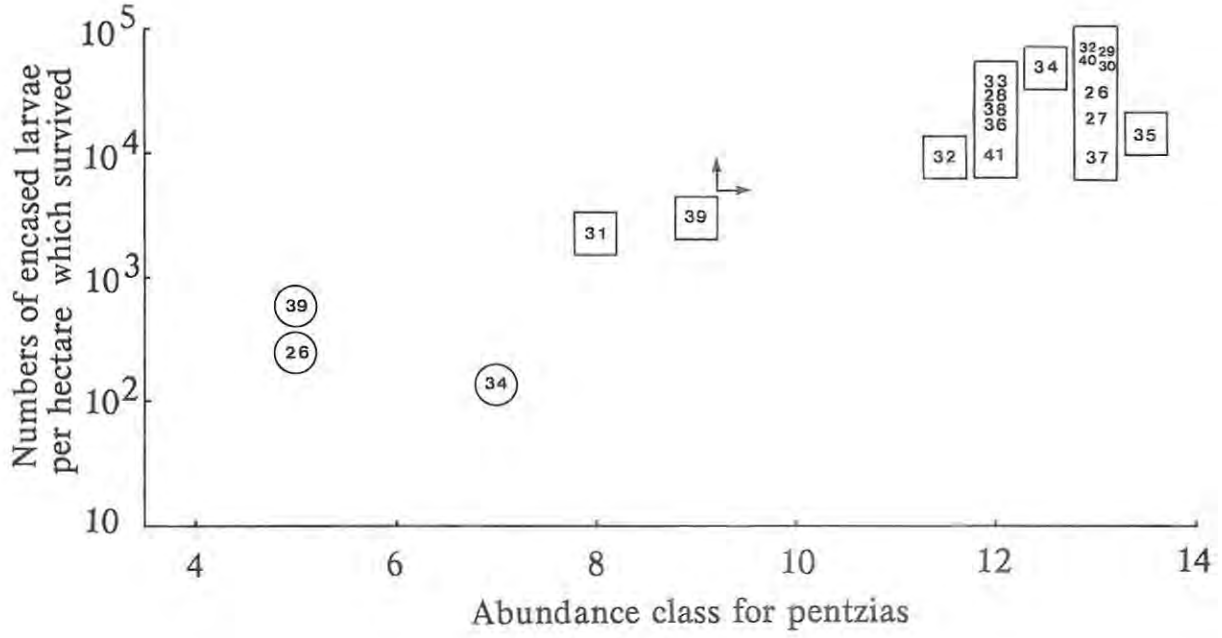

Fig. 36. The total numbers of *L. frustalis* encased larvae per hectare (see text) which survived in relation to plant abundance (Appendix 3 : Table 15) for dominant pentzias (squares) and less-dominant pentzias (circles) in the epidemic populations of the central and western Karoo. The numbering of census sites, the numbers of soil samples and the raw data are shown in Table 13. Arrows indicate underestimates of encased larvae and plant abundance due to unusually large plant sizes. Duplicated values for Site 32 are due to sub-plots.

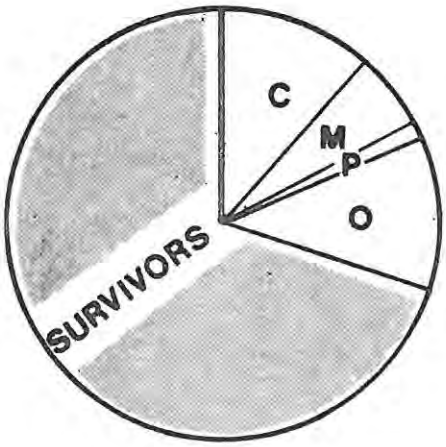

Fig. 37. The proportions of *L. frustalis* encased larvae collected from the soil under alternate food plants of *L. frustalis* for the epidemic populations of the central and western Karoo (Sites 26 - 41) killed by *Ch. curvimaculatus* (C), *M. maraisi* (M), Other Parasitoids (P) and Other Mortality (O), and the proportions which survived. The diagram is derived from the data in Table 13.

Other Parasitoids *T. picta* was the most widespread while the tachinids, especially, have not been properly studied and were sometimes more abundant than the results indicate. Marais (1955 : 62) wrote that 'It was therefore not uncommon to find Tachinid (sic) eggs on practically every *L. frustalis* larva (in the field for most of a season) ... Indeed super-parasitism by the Tachinidae was quite common'. This did not happen during the current study and it is not clear which situation is more usual. Lastly, the pathogen *B. bassiana* was widespread and prolific.

This study has identified host plants and natural enemies as major determinants of *L. frustalis* abundance. The results raise the important question of whether these factors can be manipulated to alleviate the Karoo caterpillar problem and this subject is pursued in the Discussion.

8. DISCUSSION

The Karoo caterpillar is undoubtedly a pest to those farmers who rely on pentzias and the alternate food plants of *L. frustalis* as natural grazing for their stock, but it is the expanded distribution of these plants which has resulted in the man-made Karoo caterpillar problem. There are no simple or clear-cut solutions to this impasse, which is the subject of this discussion.

Biological control was for many years regarded as the only feasible method of controlling the Karoo caterpillar under the extensive stock farming - and relatively low monetary returns per land unit - practised in the Karoo. Efforts to establish exotic parasitoids were, however, unsuccessful (Annecke & Moran 1977) and led these authors to conclude that 'All in all, we regard it as improbable that parasitoids of related species of *Loxostege* elsewhere in the world will be found that will improve, even marginally, the natural regulation of Karoo caterpillar populations that already exist in the Karoo'. The present study adds weight to their opinion since the influence of natural enemies is far more powerful than was realised in 1977.

At least three natural enemies are known to be important (Section 7 : fig. 34). *Ch. curvimaculatus* is recognised as a significant complement to the well-known parasitoid *M. maraisi*, with some evidence that it was more effective during the epidemic and pandemic outbreaks of *L. frustalis*, when parasitism by *M. maraisi* was lower. Furthermore, the pathogen *B. bassiana* is widespread and sometimes causes high mortalities in populations of *L. frustalis* encased larvae. The effectiveness of the pathogen is raised by its ability to grow saprophytically (thus ensuring a 'reservoir'

of inoculum and in this way it resembles the action of a polyphagous predator (Southwood 1977b)). Also, as noted by Southwood & Comins (1976): 'The impact of diseases on animals resembles the effects of intraspecific competition more than the natural enemies, for there is seldom an upper (limit) release point'. Collectively, the natural enemies of *L. frustalis* responded in an undercompensating direct density dependent manner in relation to the density of *L. frustalis* encased larvae. This was true for between-plant responses at both endemic and epidemic population levels and further, at epidemic levels, high-density patches of *L. frustalis* encased larvae suffered higher mortalities, indicating a further direct density-dependent response.

The impact of natural enemies, and the prospects of strengthening their action through supplementation with imported species, should be considered in relation to the overall mortality of *L. frustalis* populations, particularly the unexplained mortalities due to intraspecific competition. Predictably (Stubbs 1977), competition for food by dispersing larvae during epidemics is likely to raise the levels of mortality. Probably an even more important stochastic element in the dynamics of *L. frustalis* populations is due to the competition for host plants by adults when unfavourable conditions follow extensive larval outbreaks - like the droughts after the 1977 epidemics in the western Karoo - thus rendering plants unsuitable for subsequent generations of *L. frustalis*. The enormous numbers of moths which subsequently emerge (after overwintering) are then restricted to relatively few suitable host plants. This intraspecific competition among adults is probably not only a major cause of population fluctuations of *L. frustalis* itself, but must also affect parasitoid populations.

Due to the synchronous development of the *L. frustalis* parasitoids with that of their host (Sections 4 and 5), the effects of host-plant limitations on the parasitoids are delayed, so that large populations of overwintered parasitoids (even if previous rates of parasitism were low) also compete for comparatively low numbers of hosts and this conceivably leads to quite sudden returns to the high rates of parasitism which are characteristic of endemic populations of *L. frustalis*. On the other hand, if suitable conditions were to persist for a number of seasons, it is possible that the natural enemies of *L. frustalis* will attain an upper equilibrium level (Hassell & Moran 1976) with their host. If so, then the low rates of parasitism recorded for the so-called pandemic outbreaks of the Hanover and De Aar districts (Section 7 : fig. 34) may well be due to a temporary 'escape' by *L. frustalis* from its natural enemies. Probably an upper equilibrium level (with high rates of parasitism during outbreaks of *L. frustalis*) is sometimes prevented by the onset of unfavourable conditions in the Karoo. This illustrates a major difference between areas in which monocultures (natural or agronomic) provide a stable supply of food, and areas subjected to an unpredictable climate in which the numbers of suitable hosts fluctuate greatly between and even within seasons.

The periodic outbreaks of *L. frustalis* must be viewed in the light of the interacting roles of host plants and natural enemies. An actual situation is summarised in Table 14 and fig. 38, which show the results of the census conducted on one farm (Sites 30 - 34), following the exceptionally severe ('pandemic') outbreak recorded in the De Aar district. The data are for pentzias and the most abundant alternate food plants in the sites, some of which have

Table 14. Summary of the relationship between the abundance of *L. frustalis* and the density of its host plants (pentzias and alternate food plants) as illustrated by census data for neighbouring sites. The data are derived from the partial life tables for *L. frustalis* (Section 7 : Table 13) and the abundance classes of *L. frustalis* host plants (Appendix 3 : Table 15), with Sites 32 and 34 divided into sub-plots.

Site, Plant species	Plants per hectare		Encased larvae per soil sample		Encased larvae per hectare		Proportion of encased larvae surviving		Survivors to pupae (approximates moths due to negligible post-larval mortality)	Total yield of moths from each site
Site 32										
P. spinescens	15000	x	6,61	=	99150	x	0,67	=	66431	
W. saxitilis	300	x	4,08	=	1224	x	0,71	=	869	
										67300
Site 30										
P. spinescens	15000	x	7,18	=	107700	x	0,45	=	48465	
E. ericoides	300	x	11,90	=	3570	x	0,79	=	2820	
Pt. glauca	55	x	3,64	=	200	x	0,27	=	54	
										51339
Site 34										
P. globosa	12500	x	19,96	=	249500	x	0,22	=	54890	
W. saxitilis	Negligible									
										54890
Site 33										
P. globosa	7500	x	7,96	=	59700	x	0,64	=	38208	
R. humilis	300	x	16,77	=	5031	x	0,75	=	3773	
W. saxitilis	300	x	8,27	=	2481	x	0,71	=	1762	
										43743
Site 32										
P. spinescens	6000	x	2,17	=	13020	x	0,73	=	9505	
W. saxitilis	300	x	1,84	=	552	x	0,62	=	342	
										9847
Site 31										
P. globosa	350	x	12,95	=	4533	x	0,55	=	2493	
S. calluna	300	x	11,10	=	3330	x	0,87	=	2897	
Z. incrustatum	1250	x	21,60	=	27000	x	0,65	=	17550	
										22940
Site 34										
P. spinescens	150	x	1,20	=	180	x	0,81	=	146	
W. saxitilis	300	x	2,08	=	624	x	0,73	=	456	
										602

been divided into sub-plots for the purposes of this discussion.

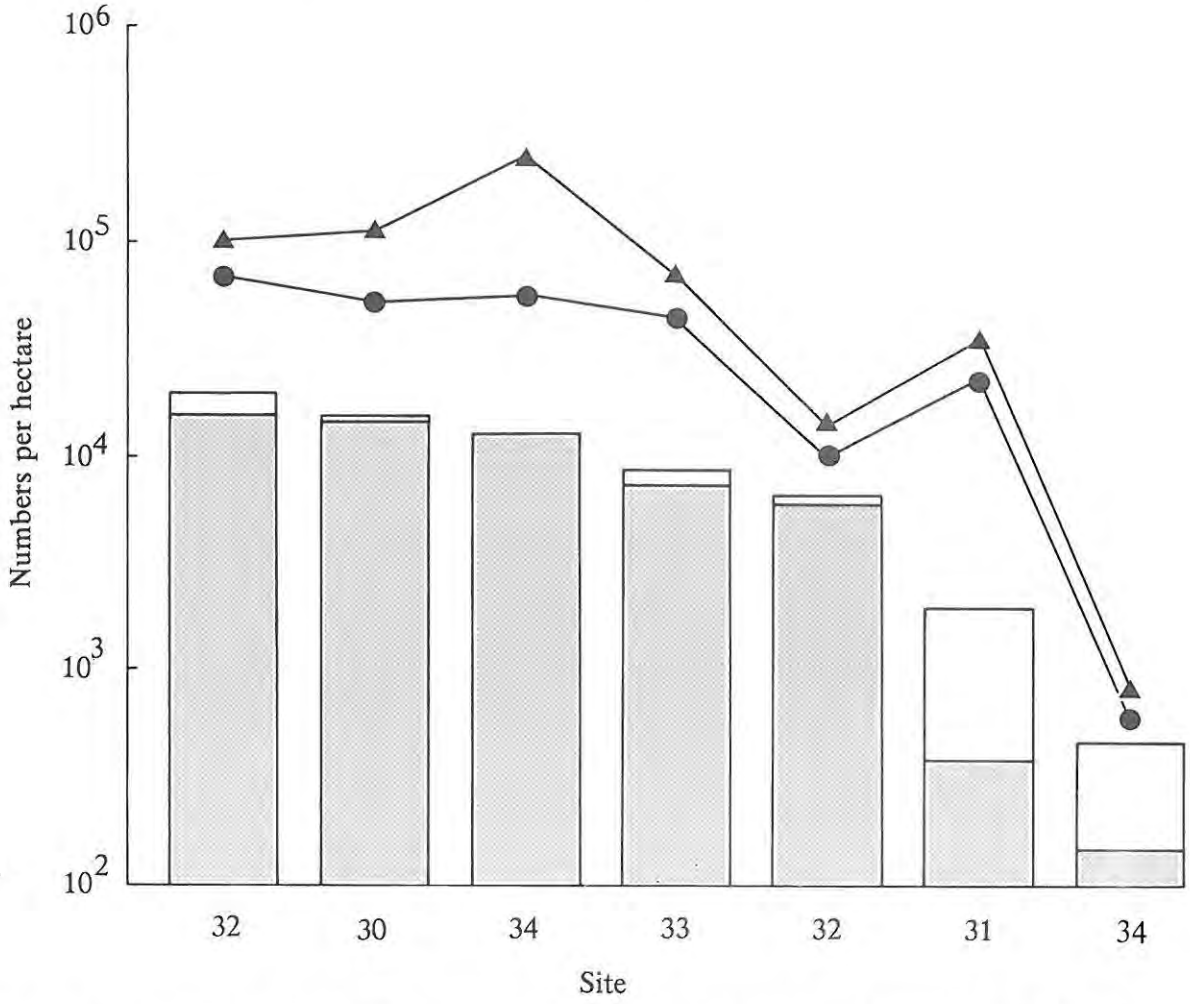

Fig. 38. The numbers of *L. frustalis* encased larvae (triangles) and 'emergent' moths (circles) per hectare in relation to the density of host plants (histogram bars - the shaded parts show the proportions of pentzias). The data are derived from Table 14.

The overriding effect of the pentzias is clear from the data in Table 14 and fig. 38. In terms of the observed host-selection behaviour of *L. frustalis*, the pentzias are attacked first and then the larvae disperse to alternate food plants. While all the material can, therefore, be allocated to the pentzias (as done here) the role of the alternate food plants, in relieving intraspecific competition among larvae, must not be overlooked. This is true for many plants which are associated with pentzias in Karoo veld.

Once *L. frustalis* larvae have entered the soil and constructed their cases it is mainly the action of natural enemies which determines the numbers of survivors. This study has shown that the natural enemies are unable to compensate for the greater numbers of encased larvae which occur in denser patches of pentzias, so that more *L. frustalis* moths are produced in veld with high densities of the pentzias. This is clearly illustrated in Table 14 and fig. 38, while it can be calculated from the data in Table 14 that the rates of mortality required to 'compensate' for the greater numbers of moths produced in the veld with higher densities of pentzias - so that each site would have produced the same number of moths - are in excess of 97% on average. Clearly, these rates of parasitism are unrealistically high - the highest rate of parasitism ever recorded for *L. frustalis* encased larvae was 92% (see Section 7 : Table 13) - and the prospects for lowering *L. frustalis* populations through reductions in plant populations, as was done in Site 34 - *P. spinescens* (Table 14 and fig. 38), are far more practicable and realistic.

It is concluded that powerful mortalities act on several stages of *L. frustalis*, among them the native natural enemies, and that further importations of natural enemies will be wasted effort. Rather, it is the sheer abundance of host plants of *L. frustalis*, together with the unpredictable climate which affects both *L. frustalis* and its parasitoids, which lead to the periodic *L. frustalis* larval outbreaks.

Reducing the numbers of host plants of *L. frustalis* is the only reasonable way of lowering *L. frustalis* populations. Furthermore, pentzias grow about a metre apart over vast areas in the Karoo (fig. 39) and due to the exponential relationship between

spacing and plant abundance (Appendix 3), this is a critical distance at which slight increases in spacing result in disproportionately large reductions in plant populations. Reducing the food supply is not a new concept in the Karoo caterpillar context (see Introduction); the feasibility of implementing such a strategy, however, requires some comment.

Fig. 39. Typical pentzia-dominant veld.

The value of pentzias and many other food plants and non-hosts of *L. frustalis* (and the management systems to propagate them), constitutes a stimulating and controversial issue. It is difficult to assess objectively the value of the pentzias, about which comments range from 'the most important fodder plants for sheep' to 'unpalatable invaders'. Karroid vegetation is usually discussed with connotations of undesirability such as 'encroachment' and 'deterioration' and it is reasonable to consider a long-term policy aimed at increasing the climax component, and a simultaneous decrease in the populations of pentzias.

This controversy about the value or otherwise of many host and non-host plants of *L. frustalis* is of immediate importance to the Karoo caterpillar project; less than clear directives will be unfair and perhaps misleading to the farming community. If pentzias are deemed to be desirable plants, then occasional damage by *L. frustalis* must be allowed for in farm management, with no alternative to farmers but to make the same provisions as for periodic droughts. If, on the other hand, pentzias are judged to be of limited value, several benefits are to hand if reductions in pentzia populations (albeit slight in terms of spacing) can be brought about:

(i) Axiomatically, the size of *L. frustalis* populations will be reduced.

(ii) Intraspecific competition among both the larvae and adults of *L. frustalis* will set in at lower population levels.

(iii) Desirable (from a grazing point of view) alternate food plants of *L. frustalis* will be less subject to damage by dispersing *L. frustalis* larvae.

(iv) Adequate methods for identifying obvious non-host plants of *L. frustalis* are available, but simple feeding trials, because they ignore some physiological aspects of development, do not provide rigid proof that *L. frustalis* will not accept them in the absence of pentzias. While I stand to be corrected on this hypothesis (as well as the host-selection hypothesis proposed for *L. frustalis* in Section 4, which is undoubtedly over-simple), the mere possibility of 'switching' must not precipitate detailed studies of the relationship between *L. frustalis* and its host plants. Such studies should be a last resort if uncertainties arise about crucial Karoo plants.

(v) Owing to the species-richness of karroid veld, substitutes for pentzias can be chosen from many other plant species.
(vi) Farmers will be less dependent upon pentzias for grazing for their stock.

Irrespective of the status of pentzias in the Karoo or long-term policies, enough is now known about *L. frustalis* (and the Karoo) to allow researchers to formulate strategies to circumvent, or at least alleviate, the Karoo caterpillar problem. The advantages of any procedures which achieve this include many of those just mentioned. A few suggestions for consideration are listed here; a team effort will undoubtedly identify additional options:
(i) It is the epidemic larval outbreaks of *L. frustalis* which are damaging. Farmers are generally unconcerned about occasional larvae, even though the webs reportedly render the plants unpalatable to stock - the effect is temporary and besides, after rains there is other food available to stock.
(ii) Veld with dense patches of pentzias is the most susceptible to attack by *L. frustalis*. These areas can be identified, with a view to employing grazing systems by which these patches (of pentzias and alternate food plants of *L. frustalis*) can be utilised by stock before outbreaks of *L. frustalis* occur. Outbreaks cannot be accurately predicted, but at least they can be expected during autumn and an abundance of moths provides some warning. Such a strategy, of course, offers no relief where entire farms consist of vegetation dominated by the pentzias.
(iii) Several undesirable plant species (e.g. *Chrysocoma* spp., *Lycium cinereum*, *Pteronia* spp.) have been identified as alternate food plants of *L. frustalis* larvae. The advantages of reducing their numbers are obvious.

(iv) The significance of non-host plants of *L. frustalis* must not be overlooked, as already observed by Marais (1955) and Nel *et al.* (1974). On one of the farms sampled during this study the pentzias were in isolated pockets which have survived a management system of grazing and veld burning to propagate grasses, none of which is eaten by the Karoo caterpillar. This illustrates a case where a farm previously susceptible to damage by *L. frustalis* is now virtually unaffected. Indeed, on the farm from which the data for Table 14 were collected, the exceptionally severe outbreaks completely defoliated the abundant pentzias and many other plant species over large areas. The damage, however, was of no consequence due to the presence of many species of grass and other non-host plants of *L. frustalis*.

Key features of the Karoo caterpillar problem are the abundant host plants, the temporary nature of damage caused by larvae and the existence of powerful native natural enemies and other mortalities. The problem can be circumvented by supplementing susceptible veld with non-host plants such as grasses and lessened by reducing undesirable alternate food plants and pentzias. The key plants are pentzias, and to assess them is clearly a research priority. Whatever the outcome of such a long-term project, alleviation of the problem must be sought in management tactics and not in further entomological research.

9. SUMMARY

L. frustalis moths fly throughout the summer months, with a peak in numbers during autumn, the rainy season in the Karoo. Due to erratic mating in field populations, moth numbers alone are of limited value in forecasting larval outbreaks. Species of *Pentzia* are selected by ovipositing females, while a variety of other plants are fed upon by larvae when they disperse under crowded conditions.

The larvae of *L. frustalis* are fully fed after about two weeks and construct protective larval cases in the soil beneath host plants, mainly near the stems. These encased larvae may enter a period of dormancy (usually for overwintering) prior to pupation and moth emergence.

Details of the interactions of the *L. frustalis* natural enemies with each other and their host and criteria for identifying and interpreting the contents of the host larval cases are presented. Parasitism generally occurs before *L. frustalis* larvae construct cases, but the parasitoids do not develop beyond the first larval instar until dormancy in the host is terminated. Consequently, nearly all the mortality of *L. frustalis* due to natural enemies (parasitoids and pathogens) is manifested in the larval cases. Individual parasitoids eventually emerge, so that the mortality data provided counts of *L. frustalis* encased larvae, mortality factors and the survivors to post-larval stages.

The mortality data are presented as partial life tables for the life-history period of *L. frustalis* between case construction and moth emergence. Post-larval mortality was found to be negligible, so that estimates of the survivors to pupae were useful. The data for live (dormant) encased larvae were obtained by dissection

and rearing and pooled with that for spent material. These partial life tables were adequate for the analysis of census data.

A census of *L. frustalis* encased larvae was conducted in various parts of the Karoo from 1975 to 1980 to represent endemic and epidemic populations and the data analysed in terms of the roles of host plants and the mortality of encased larvae. It is shown that pentzias and alternate food plants are the principal determinants of *L. frustalis* abundance, and further, that the natural enemies (especially *Ch. curvimaculatus*, *M. maraisi* and the pathogen *B. bassiana*) and other mortalities are powerful, but unable to compensate for the expanded distribution of the host plants of *L. frustalis*.

A strategy to alleviate the Karoo caterpillar problem is presented, and relies on reductions in the populations of host plants of *L. frustalis*. The feasibility of this strategy, particularly in respect of pentzias, depends upon the value of the plants in Karoo pastures. An assessment of the value of the pentzias as grazing for stock and the prospects for a reduction in pentzia density seem to be research priorities for botanists and pasture scientists. It is concluded that any further entomological research input will be wasted effort since there is virtually no hope for alleviation of the Karoo caterpillar problem using biological control methods, and that a solution may be found in a different approach to farm management.

APPENDIX 1. An artificial diet for *L. frustalis* larvae.

A modified Shorey & Hale (1965) meridic diet was made up as follows:

Ingredient	Quantity
Dry, finely powdered *Pentzia* spp. leaves	6 g
Kidney beans, soaked overnight in distilled water	44 g
Wheat germ	10 g
Brewer's yeast*	10 g
Ascorbic acid	1 g
Formaldehyde (40%)	0,6 ml
para-Hydroxy-methyl-benzoate	0,6 g
Potassium sorbate	0,6 g
Agar	3 g
Distilled water	300 ml

The ingredients, excluding the Agar, were homogenised in half the volume of water for 3 - 5 min at medium blending speed. The agar was added, melted in the rest of the water, and the mixture blended again.

The most suitable containers for rearing were 250 ml waxed-paper cups** with about 20 g medium, sufficient for 10-20 larvae.

The medium is suitable for transient rearing, but not for continuous cultures (see Section 4). Up to six generations have been maintained on the medium.

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* 'Gold Star' manufactured by Union Yeast, Industria.

** Manufactured by Mono Containers, Maitland.

APPENDIX 2. Mean nightly catches of *L. frustalis* adults in a light trap at Middelburg. Data up to June 1966 is from Wolmarans (1968). Raw data for July 1966 to June 1974 on file, Plant Protection Research Institute, Middelburg. All data are quoted as 'Robinson' values.

Year	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1964							0	0	27	2965	2300	5794
1965	3170	3917	1198	619	9	0	0	0	5106	774	2760	214
1966	223	414	7479	9	0	0	0	0	5	323	5247	8349
1967	12298	18611	6409	560	5	0	0	0	342	1421	3867	542
1968	1221	278	19139	742	5	0	0	0	150	3252	6003	2833
1969	1831	269	3412	191	0	0	0	0	228	7893	17837	8039
1970	173	4254	1877	556	0	0	0	0	77	1508	5010	11510
1971	11004	8536	3580	164	0	0	0	0	200	8267	2091	1658
1972	2082	4241	13122	1266	0	0	0	0	146	5202	12215	503
1973	530	26198	57481	15864	8	0	0	0	34	27516	22041	8516
1974	34676	50179	11112	40	3	0	0	0	0	35	289	257
1975	92	1388	2586	139	0	0	0	0	3	77	360	2016
1976	10027	16170	1749	52	0	0	0	0	1	24	111	27
1977	40	7354	4149	25	0	0	0	0	10	582	392	1068
1978	1197	546	1030	29	0	0	0	0	7	1100	204	920
1979	6951	955	2596	267	0	0	0	0	229	1743	1849	393
1980	194	806	4768	339	1	0						

Note:

(i) When the two traps were operated concurrently (Section 3) the nightly means were correlated (r = 0,86: $P < 0,01$.) After transformation to Log (nightly means +1) r = 0,95. In order not to affect the trend between months for the trapping period, a linear correction factor (x 4,5548) was applied to all 'Wolmarans' values to convert the data to 'Robinson' values (Section 3). Data for July 1972 to June 1974 are means between the trap types. Similar data were recorded by Annecke & Moran (1977: fig. 3) except that all the data were transformed to 'Wolmarans' values.

(ii) Comparisons between seasons before and after 1974 are restricted by the transformation of data and different trap localities (Section 3).

(iii) The trap was considered operative for only eight nights during March 1967; the remaining catches were discarded as uncountably large. The data cannot be reliably corrected - there

is no record of other species present at the time - but it is accepted that the figure presented is an underestimate. Adjustments (Section 4) were made as if the nightly catch for March 1967 was equal to the highest recorded catch from a Wolmarans trap.

APPENDIX 3. Descriptions of *L. frustalis* census sites

The objective is to describe the census sites, especially the vegetation, in broad terms. Many methods of description are available (Brown 1954; Cain & Castro 1959; Mueller-Dombois & Ellenberg 1974). The nature of the sites necessitated a rapid method but expressed in the same terms as intensive studies: this is a general requirement for vegetation studies (Dix & Butler 1960). The method adopted here was essentially that of Acocks (1975), that is the recognition of abundance classes, but it differs in so far as estimates were made from the numbers of plants rather than their spacing. The abundance classes* are shown in fig. 40. They differ slightly from those of Acocks (1975) to provide greater sensitivity in the region of one plant per square metre and because the non-linear relationship between density and spacing is allowed for.

Quadrats of 100 m² were the basis of the method, a convenient and adequate plot size for karroid veld (Werger 1973). Multiples or fractions of such plots (e.g. belt transects) are easily demarcated or visualised in the field; the size (and replications) are dictated by the abundance and distribution of a species. By adapting the plot size only a few categories (up to about 50 plants) are needed. In practice most entries are made from actual counts of relatively few plants. Estimates of the spacing of plants are a useful adjunctive method (Acocks 1975),

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* Calculated from $m = 1/r^2$ where m is the density per unit area and r the distance between evenly spaced plants. Compare with $m = 1/4r^2$ (Clark & Evans 1954) for random nearest-neighbour measurements.

particularly for the lower abundance classes (fig. 40), where relatively large increases in spacing affect numbers. In karroid veld, dominant species often grow about a metre apart (= 10 000 plants/ha) and this spacing is a useful point from which to start.

Abundance is not applied in its strict sense in Table 15. Some species which occur in isolated dense clumps (e.g. stonoliferous grasses) and annuals which are present for brief periods only - both of which may be extremely abundant in actual counts - are relegated to lower classes. Also, seedlings are mostly ignored in order to illustrate 'typical' (defined in Section 6) plants. It is only for the rarer species that seedlings are noteworthy as pointers to veld condition. The species lists (Table 15) are undoubtedly incomplete since the surveys were extensive, and further, although multiple visits are a necessity in areas with erratic rainfall (Werger 1973), this was not always possible during the study. All records were collected by me. Separate lists of sites compiled at different times revealed no obvious difference in the structure of communities; tests between different operators have not been done. Precise density counts (by various people) were made in several sites and compared to previous estimates. Very few discrepancies were found and then only between adjacent classes. In fact, a much more sensitive procedure is probably practicable. Karroid veld lends itself to rapid-counting techniques; the Braun-Blanquet method (Poore 1955) has been successfully applied by Werger (1973). With the Acocks (1975) method precise density counts are conveniently combined with estimates of less abundant (or less important) species.

Some taxonomic difficulties are not evident from Table 15. Hybrids between *Eriocephalus aspalathoides* DC., *E. spinescens* and *E. pubescens* DC. are listed under the genus for the Carnarvon sites. The *P. globosa* in Site 39 are hybrids with *Pentzia pinnatisecta* Hutch. and *P. spinescens*. *Chrysocoma polygalifolia* was detected in Site 39 later than the census dates (Section 6). While the two species of *Chrysocoma* occurred in about equal numbers, the census data could not be apportioned.

Some other salient features of the census sites are shown in Table 16.

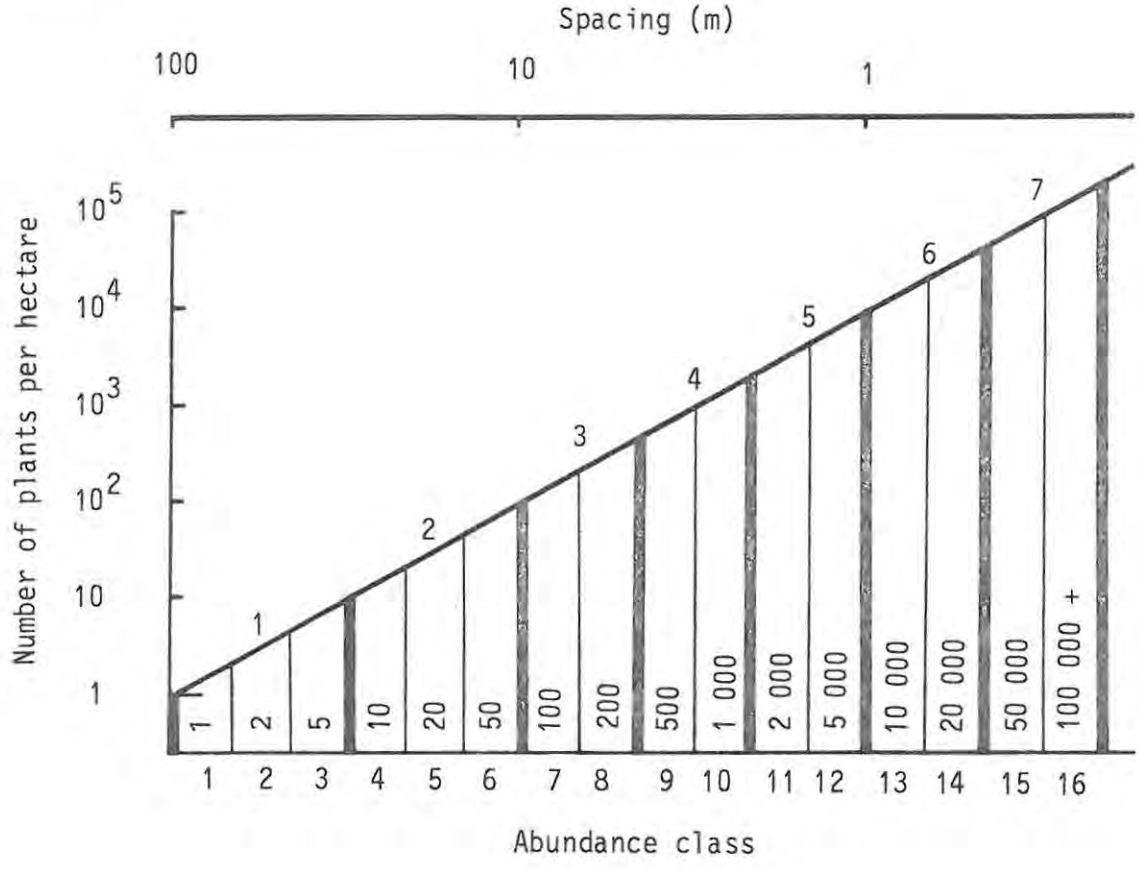


Fig. 40. The numbers of plants in abundance classes. Lowest values for each class are shown below the diagonal. The classes applied in Table 15 are shown above the diagonal and demarcated by thicker lines.

Table 15. Botanical composition of census sites and the status of plants as hosts of *L. frustalis*. Abundance classes are explained in fig. 40. Dominant and co-dominant species (+) are shown for extensive sites. Host-status terminology is explained in Section 3.

Species	Host status	MIDDELBURG 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	CRADOCK 24	ADELAIDE 25	RICHMOND 26	27	HANOVER 28	29	DE AAR 30	31	32	33	34	VICTORIA WEST 35	CARNARVON 36	37	38	39	40	41
ACANTHACEAE																																										
Blepharis villosa (Nees) C.B. Cl.	?															1				1			1	1																		
AIZOACEAE																																										
Galenia procumbens L.f.	Non-host		+		3	3	1	1	2													2	2	1			1	1		2	1	2		1	1					1	1	1
Gisekia L.	?							1																																		
Limeum aethiopicum Burm.	Negligible										1																														1	
Plinthus karooicus Verdoorn	Negligible				2	1	2		1	1														1			2	1	1	4	2		1			1	1	3	1	1	3	1
Tetragonia arbuscula Fenzl	High				2	1			1																		1	1			1	1					1			1		1
AMARANTHACEAE																																										
Amaranthus thunberghii Moq.	?				1			1																																		
ANACARDIACEAE																																										
Rhus undulata Jacq.	?							2														1																				
ASTERACEAE																																										
Berkheya atractyloides (L.) Schltr.	High				1		1																3						1	1	1	1	1	1	2	2		1	1	2	2	
Chrysocoma polygalifolia S. Moore	?																																							3		
Chrysocoma tenuifolia Berg.	Low				1			2	1	3	1		2	1		1	2	1	1	2		2	1	2			3	2	1	1	1			2	1	1	2	1	3	3		2
Cirsium vulgare (Savi) Ten.	?																						3	2																1		
Dimorphotheca cuneata (Thunb.) Less.	Negligible						1				1			1		1		1	1																							
Dimorphotheca zeyheri Sond.	?				1																																					
Elytropappus rhinocerotis (L.f.) Less.	Intermediate										1		1	1	1	1	1	2	2	2	2		1																			
Eriocephalus L.	?																										1										1	2		2	2	3
Eriocephalus ericoides (L.f.) Druce	High	+	+		2	2	5	1	4	5													1	2			1	1	2	2	3		2	2	1	1	1	1	2	1	2	2
Eriocephalus spinescens Burch.	High				1	1	2		1	2																	3	2	2	1						4	4	2	4	2	2	
Euryops lateriflorus (L.f.) DC.	Negligible																																	1								
Euryops multifidus (Thunb.) DC.	?																																									1
Euryops oligoglossus DC.	?													1	2	1	1	1	2	1	2																					
Felicia filifolia (Vent.) Burtt Davy	Intermediate				1	1	1	1																			3										1					
Felicia muricata (Thunb.) Nees	Intermediate				1	1	2	2			4	2	1	2						1		3	2	2	1		2				1				2	1	1				4	
Geigeria filifolia Matt.f.	?																						1																			
Gnaphalium luteo-album L.	?						1																3	1											1						1	1
Helichrysum Mill.	?										2	1	1	1	1	1	1		1	1	1				1											1						
Helichrysum lucilioides Less.	Low						2																	1																		
Helichrysum parviflorum (Lam.) DC.	Low						1	1	1											1	1																					
Helichrysum pentzioides Less.	Negligible				1	1																1					1															
Hertia pallens (DC.) Kuntze	Negligible				3	1			1													1					1				1	1										1
Osteospermum L.	?				1										1	1	1																									
Osteospermum leptolobum (Harv.) Norl.	Intermediate				1		2	1		1												1	2	1					1		1		2	1	2							
Osteospermum spinescens Thunb.	Low				1																									1										1	2	
Pegolettia retrofracta (Thunb.) Kies	Negligible																														1		1							1		
Pentzia Thunb.	High																																1					1			2	
Pentzia globosa Less.	HOST PLANT	+	+		2	5	2	2	5	4	5	6	5	6	6	5	6	5	6	4	6	2	2	2			2		5	6	3	3	2	5	4					4		
Pentzia incana (Thunb.) Kuntze forma	HOST PLANT	+	+	+	5	2	1	3	1	1												6	5	5	6	+	2	1								1				2		
Pentzia lanata Hutch.	High				1	1	1	2	1	1																							1									
Pentzia punctata Harv.	High							1																																		

Table 15 (cont.)

Species	Host status	Site																																								
		MIDDELBURG 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	CRADOCK 24	ADELAIDE 25	RICHMOND 26	27	HANOVER 28	29	DE AAR 30	31	32	33	34	VICTORIA WEST 35	CARNARVON 36	37	38	39	40	41
Pentzia spinescens Less.	HOST PLANT																										6	6	4	1	6	2	5	2	3	6	5	6	5	2	6	5
Phymaspermum aciculare (E. Mey. ex DC.)	Negligible				1																																				1	
Phymaspermum parvifolium (DC.) Benth & Hook.f.	High				2	1	1	1	1	1												2		2	1		2	1	2	1					1							
Pteronia L.	?													1																										1		
Pteronia erythrochaeta DC.	?				1																																					
Pteronia glauca Thunb.	Low				2	1	2		1	1																	1	1	1	1	2	1	1	1			1	1	1	1	2	2
Pteronia glomerata L.f.	?																							2																		
Pteronia mucronata DC.	?																																						1			
Pteronia punctata Phill.	?				1																																					
Pteronia sordida N.E. Br.	Intermediate				1	1	1		1	2																	2	2			1					1	1	2	2		2	
Pteronia tricephala DC.	Negligible				1		1		1	2	1	2	1	2									1						1	1	1											
Pterothrix spinescens DC.	Low?				1	1	1		1														1	1				2	1	1					2							1
Rosenia Thunb.	?								1	1															1		1	2	1					1		2		1			1	
Rosenia humilis (Less.) Bremer	High				2	1	2		2	2												2	2	2			2	1	3	3	1		2	3				1	2	2		1
Rosenia oppositifolia (DC.) Bremer	?																										1		1													
Schkuria pinnata (Lam.) Kuntze ex Thellung	?							1																																		
Senecio leptophyllus DC.	High				1																1		1				1															1
Tagetes minuta L.	Negligible							1																																		
Tarchonanthus camphoratus L.	?							1																																		
BIGNONIACEAE																																										
Rhigozum obovatum Burch.	?																																						1			
BORAGINACEAE																																										
Lappula echinata Gilib.	?								2																																	
Lithospermum cinereum DC.	?																						1																			
BRASSICACEAE																																										
Lepidium africanum (Burm.f.) DC.	?						1						1							1					1				1	1				1	1				1	1	1	1
CAMPANULACEAE																																										
Lightfootia tenella Lodd.	Low				1								1																		1		1		2							
CHENOPODIACEAE																									2																	
Atriplex semibaccata R. Br.	High				1	1																	2	1	1		1	1														
Atriplex suberecta Verdoorn	High					1		7	1		1																					1			1							
Chenopodium L.	?					1			1																																	
Chenopodium glaucum L.	?																																						1	1		
Exomis microphylla (Thunb.) Aell.	?																											1														
Kochia Roth	?				1		1																				1												2	2		
Salsola L.	Low																										1															
Salsola aphylla L.f.	Negligible																										3	1												1		
Salsola calluna Drège	Intermediate				4	2	1		1	1												2	2	1			1	1	1			3		1	1				1	1		
Salsola glabrescens Burtt Davy	Negligible						1																								2	3			1							
Salsola kali L.	Low				1	1																													1					1		
Salsola rabieana Verdoorn	?																																							1		4
Sasola tuberculata (Fenzl ex Moq.)	Negligible																																			3	1	2	2	1	3	
EBENACEAE																																										
Diospyros austro-africana De Wint.	?																													1												
Diospyros lycioides Desf.	?							2														1																				
EUPHORBIACEAE																																										
Euphorbia L.	?																																									

Table 15 (cont.)

Species	Host status	MIDDELBURG 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	CRADOCK 24	ADELAIDE 25	RICHMOND 26	27	HANOVER 28	29	DE AAR 30	31	32	33	34	VICTORIA WEST 35	CARNARVON 36	37	38	39	40	41
FABACEAE																																										
Acacia karroo Hayne	?																						1	1	1																	
Aspalathus L.	?										1																															
Indigophera alternans DC.	Negligible							1																									1									
Indigophera sessiliflora DC.	Non-host						1		1																																	
Melolobium candicans (E.Mey.) Eckl. & Zeyh.	Negligible																										1	2											1	1		2
Melolobium microphyllum Eckl. & Zeyh.	Negligible							2			2		1	1			1	1	1	2	2																					
Sutherlandia frutescens R. Br.	?																											1														
Wiborgia Thunb.	?																																					1		2		1
GERANIACEAE																																										
Sarcocaulon salmoniflorum Moffett	?																											1								1						
IRIDACEAE																																										
Homeria pallida Bak. and *Moraea polystachya* Ker-Gawl.	?						1			2												1	1					1									1					
LAMIACEAE																																										
Salvia verbenaca L.	Intermediate				1	1	1	1	1	1												1		2	2		1		1	1			1	1	2					2	1	
Stachys rugosa Ait.	Non-host						1	2	1																						1		1							1		
LILIACEAE																																										
Asparagus spp. mainly *A. suaveolens* Burch.	Non-host				2	1		1	1	1	1			1		1				1	1	2		1			1	1	2	2	2	2	2	2	2	2	2	2	3	3	1	2
Bulbine frutescens (L.) Willd.	?													1						1																						
MALVACEAE	?																															1				1						
MELIANTHACEAE																																										
Melianthus major L.	?																					1													1							
MESEMBRYANTHEMACEAE	?																								5																	
Delosperma tuberosum Schwant.	Non-host				2				1															1	2		1			1		1		1		1						
Drosanthemum lique (N.E. Br.) Schwant.	?				1																						1															
Eberlanzia spinosa (L.) Schwant.	Non-host				1	1	1	1	2	1												1	2		1		1	2	1	2	2		1		1	1	2		1			
Psilocaulon N.E. Br.	Non-host					1																			2		1	1								1	1	2		1		
Ruschia grisea (L. Bol.) Schwant.	?				1																																					
Trichodiadema pomeridianum L. Bol.	Non-host					1																							1		1											
PAPAVERACEAE																																										
Argemone mexicana L.	?																							2																		
POACEAE																																										
Aristida diffusa Trin.	Non-host				1	1			2	1													1	2						1	1				1						1	
Aristida congesta Roem. & Schult.	Non-host				1	1	1			2			1									2	3	2			1	2	4	3	2	7	5	5	6	3						2
Bromus japonicus Thunb.	Non-host								1																																	
Bromus unioloides H.B. K.	Non-host										1		1		1																											
Chloris virgata Swartz	Non-host				2	1		2		2												2	4	4	2		1	1	1			6	1	6								
Cymbopogon plurinodis (Stapf) Stapf	Non-host								1																																	
Cynodon incompletus Nees	Non-host	+			2	7		2	2	1	3	7	6	7	1	7			5			6	3	3					6	7		6	1	7	1							
Digitaria spp. mainly *D. eriantha* Steud.	Non-host						3	1	6	2																				1										2		
Enneapogon Desv. ex Beauv. and *Schismus* Beauv.	Non-host				1	1	1			1														1			1	2	7	1	7	2	4	7	4	3	7	7	7	7	7	6
Eragrostis bergiana (Kunth) Trin.	Non-host				1	1	1			1																			1	1	2							1		1	4	
Eragrostis bicolor Nees	Non-host				2	1	1		2	1	4	3	6						3		3	1	3	1	1		1			1				1								
Eragrostis spp. mainly *E. curvula* (Schrad.) Nees	Non-host	+		+	2	2	2	3	6	1	5		6	2	2		2	4	2	1	2	1	2	2	5					2			5	1		1			2			1
Eragrostis lehmanniana Nees	Non-host	+	+	+	5	2	6		5	2			1			1						2	3	2			2	5	2	2	2	3	5	2	7			2		1		5
Eragrostis obtusa Munro ex Fical. & Hiern	Non-host				3	2	5		4	2				2								1	3	2	1		1	2	2	1	1	1	1	6	2	1				1		2
Fingerhuthia africana Lehm.	Non-host							1																																		

Table 15 (cont.)

Species	Host status	MIDDELBURG 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	CRADOCK 24	ADELAIDE 25	RICHMOND 26	27	HANOVER 28	29	DE AAR 30	31	32	33	34	VICTORIA WEST 35	CARNARVON 36	37	38	39	40	41
Karroochloa purpurea (L.f.) Conert & Türpe	Non-host										6	7	2	7	4			2	2	2	2																					
Melica decumbens Thunb.	Non-host				1	1		3	1	1	2	2	1	2	2		1	1	1	1									1		1											
Merxmuellera spp. mainly *M. disticha* (Nees) Conert	Non-host										2	2	6	2	1		5	4	5	6	4																					
Panicum stapfianum Fourc.	Non-host				2				2																																	
Sporobolus fimbriatus Nees	Non-host				2	2	2	3	3	1				2							1	1	1							1												
Stipagrostis ciliata (Desf.) De Wint.	Non-host																																					2	1	1	1	
Stipagrostis namaquensis (Nees) De Wint	Non-host																																							1		
Stipagrostis obtusa (Del.) Nees	Non-host				1																						1	1			1		1	3		2	1	5	4	3	6	7
Tetrachne dregei Nees	Non-host					1	2				6		2		1			1	1	1																						
Themeda triandra Forsk.	Non-host						1		2		1		1							1																						
Tragus koelerioides Aschers.	Non-host				2	1	2		1	2													2	1					6					1								
Tragus racemosus (L.) All.	Non-host				2	1		1																				1														
POLYGALACEAE																																										
Polygala L.	?												1														1														1	1
RUBIACEAE																																										
Anthospermum L.	?																																									1
Nenax microphylla (Sond.) Salter	Negligible				1	1			1												1		2	2											1							
SANTALACEAE																																										
Thesium hystrix A.W. Hill	Non-host				1	1			1	1												2	3		1											1	1	2	2	1		1
SCROPHULARIACEAE																																										
Aptosimum Burch.	?					1																															1					
Aptosimum depressum Burch.	Non-host				1	1			1	1												2	1	2			1	1	2						1	1			2			
Aptosimum steingroeveri Engl.	?																																			2					1	3
Peliostomum leucorrhizum E. Mey. ex Benth.	Non-host																														1							4			4	
Sutera Roth	?									2																																
Sutera atropurpurea (Benth.) Hiern	Negligible																																									1
Sutera pinnatifida Kuntze	?																														1		1		2							
SELAGINACEAE																																										
Selago L.	?																			1								1													2	3
Selago albida Choisy	Negligible																										1															
Selago speciosa Rolfe	?							1																																		
Walafrida geniculata (L.f.) Rolfe	High				2	1		2		1						1						2		2			1			1		1										
Walafrida saxitilis (E. Mey.) Rolfe	High				1	1	1	2	1	1	2	4	3	2	2	2	2	2	3	2	6	2	2	2					5	4		1	3	3	3							
STERCULIACEAE																																										
Hermannia cuneifolia Jacq.	Low																										1	1	1													
Hermannia spinosa E. Mey. ex Harv.	?																																							1		
Hermannia vestita Thunb.	Negligible					1																																		1		
SOLANACEAE																																										
Lycium cinereum Thunb. agg.	High		+		3	2	1	3	2	3	1		1	1								1	2	1	1		3	1	2	2	2	2	2	3	2	1	1	3	2	3	3	1
THYMELIACEAE																																										
Gnidia polycephala (C.A. Mey.) Gilg	Non-host				2																							2			1				1			1			2	1
Passerina L.	?										1				1	2	1		1	2	2																					
ZYGOPHYLLACEAE																																										
Tribulus terrestris L.	Non-host				1	1		2																						1												3
Zygophyllum L.	?																																					2		1	2	
Zygophyllum gilfillani N.E. Br.	?																														2								1			
Zygophyllum incrustatum E. Mey.	High				1				1	1												5	4	3								4			1	1						
Zygophyllum retrofractum Thunb.	Low																																				2	2		1	2	

Table 16. Salient features of census sites. Topographical terminology is adapted from Roux (1968).

Feature	MIDDELBURG																							CRADOCK	ADELAIDE	RICHMOND		HANOVER		DE AAR					VICTORIA WEST	CARNARVON					
Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
AREA (ha)																																									
1 - 5	-	-	-	-	-	-	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	+	+	+	-	+	+	+	+	-	+	+	-	+
5 - 20	-	-	-	+	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	+	-	-	-	+	-	-	-	-	+	-	-	+	-
20 - 200	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TOPOGRAPHY																																									
Mountain veld, mainly slopes	+	-	-	-	-	-	+	-	-	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apron veld, hilly	+	+	+	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	+	-	+	-	-	+	-	-	-	-
Plains and 'leegtes' (hollows)	-	+	+	+	+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	-	+	+	+	+	+	+	-	+	+	-	+	-	+	+
Flood course	+	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-
SOIL																																									
Mainly clayey, difficult to sift	-	+	-	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	+	-	-	-	-	-	+	-	+	-	-	-	-	-	+	-	-
VELD																																									
Typical karroid veld	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	-	+	+
Uniform	-	-	-	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	+	+	+	+	+	+	-	+	-	+	+	+	+	-	+	+
Main hosts sampled overgrown	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
GENERAL																																									
Recent *L. frustalis* larval outbreaks sampled	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	+	+	+	+	+	+	+	+	+	-	-	+	+	+	+	-
Neighbouring sites with equal symbols	a	b		b	b	b	a	c	c	d	d	d	d	d	d	d	d	d	d	d	e	e	e			f	f	g	g	h	h	h	h	h			i	i	i		

APPENDIX 4. The identification of immature larvae of *L. frustalis* parasitoids.

CHARACTERISTICS OF FIRST-INSTAR PARASITOID LARVAE (FIGS 41 - 46)

Vesiculate (fig. 41) ..... *Ch. curvimaculatus*

Polypodeiform (fig. 42) ..... *Cr. frustalis*

Mandibulate (figs 43 - 44) ..... *M. maraisi*

Caudate (fig. 45) ..... *T. picta*

Pigmented planidium (fig. 46) ..... *Pr. rostratus*

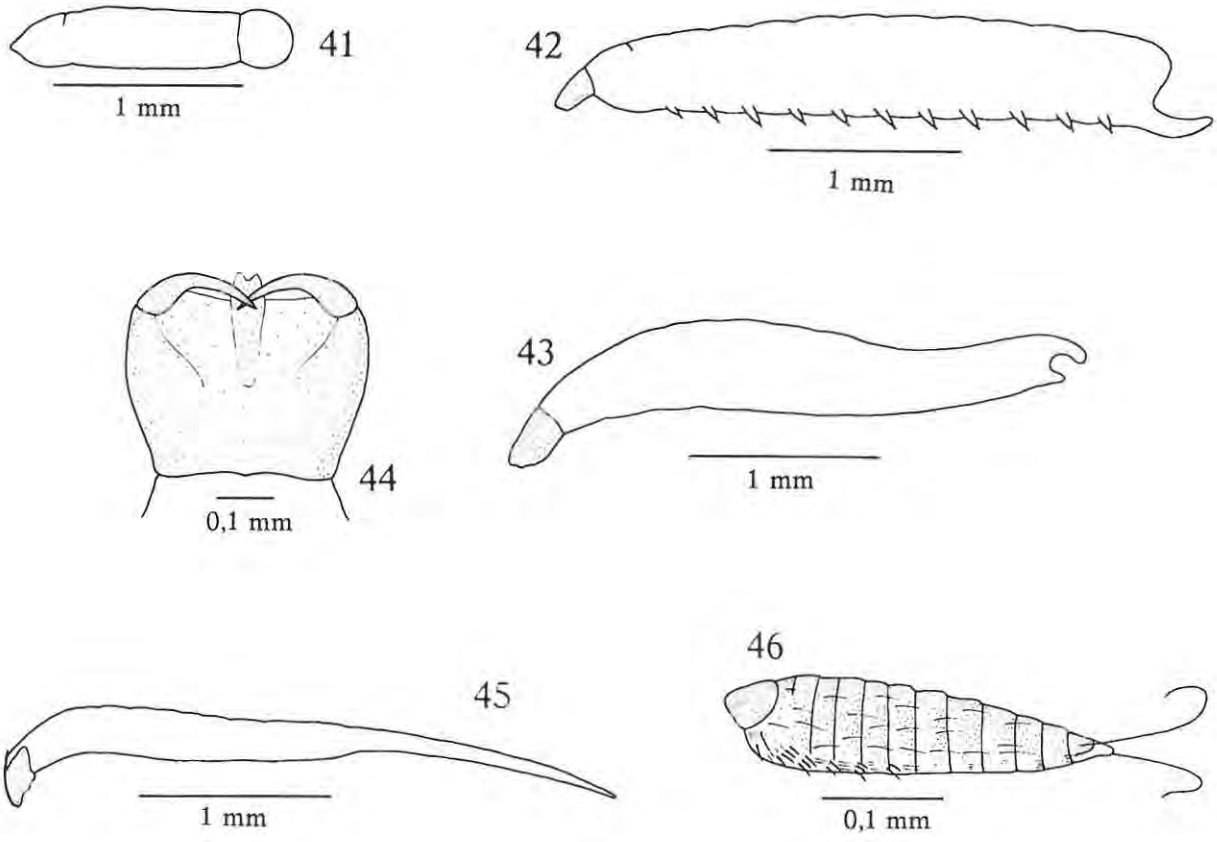
Unpigmented planidium ..... *bombyliids*

The terminology is mainly that of Clausen (1940). 'Caudate' is reserved for *T. picta* (fig. 45), although according to Hagen (1964) the anal process (Allen 1962) of *M.maraisi* (fig. 43) would qualify it as caudate. 'Mandibulate', however, is more convenient and appropriate for *M. maraisi* (fig. 44).

The FIRST-INSTAR LARVAE of *L. frustalis* parasitoids are all dissimilar and easy to recognise when alive. The primary hymenopterous parasitoids are usually forced out of the host during dissections and wriggling movements make them conspicuous. The pigmented planidia of *Pr. rostratus* (fig. 46) contrast sharply with their pale-coloured hosts, but unfortunately not with the dark *L. frustalis* integument. Pigmented planidia are peculiar to the perilampids and eucharids (Short 1952); since the latter are not associated with *L. frustalis*, *Pr. rostratus* identifications are made easy. Remains of first-instar parasitoid larvae are less easy te detect. Head capsules must be searched for, which is practical only for *M. maraisi* (figs 43 - 44) and, to some extent, *T. picta* (fig. 45).

First-instar larvae of the chalcidids and *St. breviscapus* have not been found. Descriptions of representatives of the families (Clausen 1940; Coseglia *et al.* 1977; Parker 1924) suggest that the chances of confusing them with other *L. frustalis* parasitoids are remote.

Identification of INTERMEDIATE-STAGE LARVAE of the *L. frustalis* parasitoids can virtually be eliminated by the timing of dissections so that a complete study is not justified. Two species have been described, namely the vesiculate and caudate larvae of *Ch. curvimaculatus* and *T. picta* respectively (Broodryk 1967, 1969).

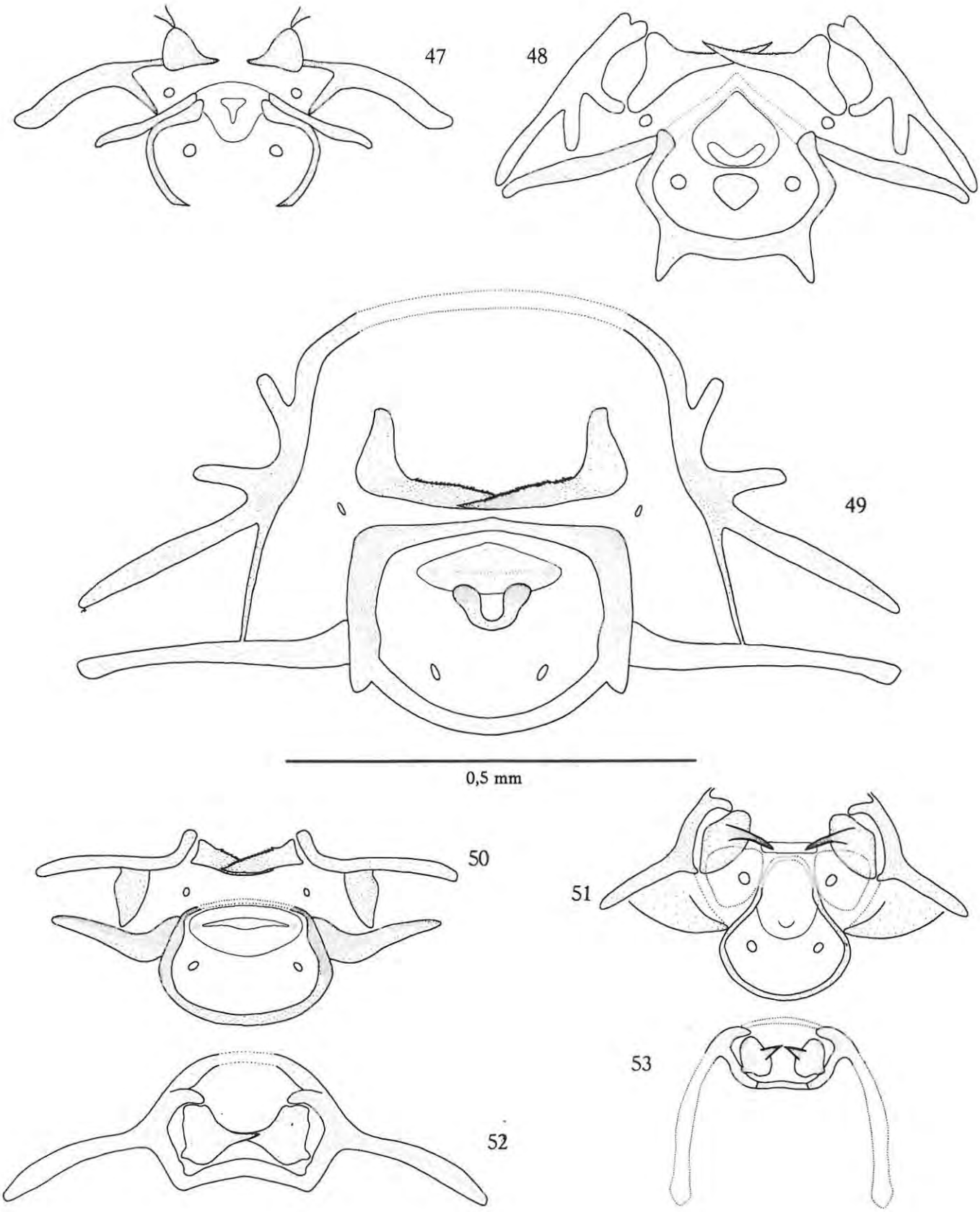


Figs 41 - 46. *L. frustalis* parasitoids. First-instar larvae. 41. *Ch. curvimaculatus*. 42. *Cr. frustalis*. 43 - 44. *M. maraisi*. 45. *T. picta*. 46. *Pr. rostratus*.

APPENDIX 5. The identification of mature larvae of *L. frustalis* parasitoids.

KEY TO THE MOUTHPARTS OF MATURE LARVAE OF HYMENOPTEROUS PARASITOIDS (FIGS 47 - 53)

1. Maxillary and labial areas differentiated 3
2. Maxillary and labial areas undifferentiated 7
3. Labial sclerite discontinuous (fig. 47) ..... *T. picta*
- Labial sclerite continuous 4
4. Labial processes present (fig. 48) *M. maraisi*
- Labial processes lacking 5
5. Epistoma and pleurostomae elaborate (fig. 49) ..... *Cr. frustalis*
- Epistoma and pleurostomae simple 6
6. Hypostomal spurs present; labial sclerite distinct, transverse; most sclerites distinct (fig. 50) .... *Ch. curvimaculatus*
- Hypostomal spurs lacking; labial sclerite convex; all sclerites except mandibles indistinct (fig. 51) ..... *St. breviscapus*
7. Pleurostomae and hypostomae distinct (fig. 52) ..... *Pl. capensis*
- Pleurostomae and hypostomae indistinct (fig. 53) ..... *Pr. rostratus*



Figs 47 - 53. *L. frustalis* parasitoids. Mouthparts of mature hymenopterous larvae, anterior aspects. 47. *T. picta*. 48. *M. maraisi*. 49. *Cr. frustalis*. 50. *Ch.curvimaculatus*. 51. *St. breviscapus*. 52. *Pl. capensis*. 53. *Pr. rostratus*.

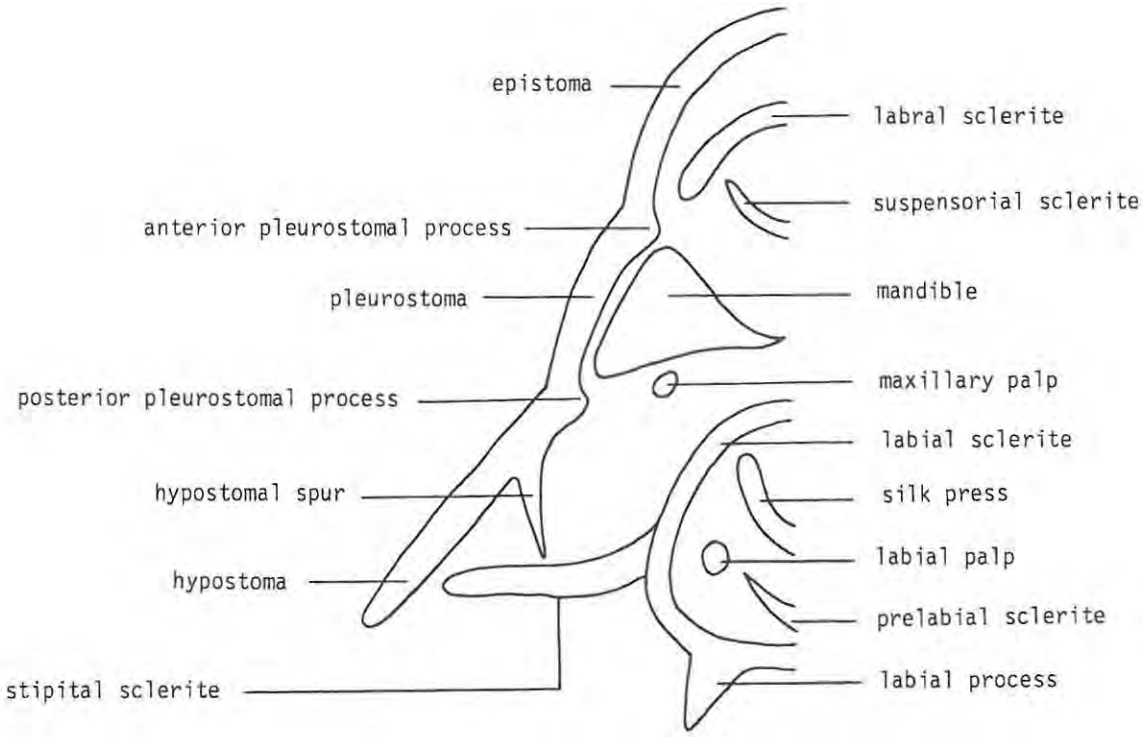


Fig. 54. A generalised diagram of the mouthparts of mature hymenopterous larvae. Partly after Finlayson (1960).

The terminology of Short (1952) for the mouthparts of mature hymenopterous parasitoids is used (fig. 54). A number of characters require general and specific comment.

The term 'distinct' is reserved for clearly-sclerotized structures. The drawings in figs 47 - 53 are somewhat misleading since they are made from specimens mounted flat, so that some structures are unrealistically clear. This is particularly true for the mandibles - it is only in *St. breviscapus* (fig. 51) that they are distinct in live specimens - hence their omission from the key. The generalisation that mandibles are toothed in ectoparasitoids and simple in endoparasitoids (Hagen 1964; Short 1959) does not hold for the hymenopterous parasitoids of *L. frustalis*. Both conditions exist in the endoparasitoids while the sole known ectoparasitoid *Pr. rostratus* (fig. 53) has simple mandibles. The

maxillary and labial palps are figured. However, they are useful only for orientation, not for the couplets. Similarly, this is the case with the silk presses and prelabial sclerites which tend to vary in shape, position and clarity, probably through distortion during mounting.

Macrocentrines are characterised by reduced hypostomal spurs (Čapek 1970; Short 1952). This is not so in *M. maraisi* (fig. 48) in which they almost reach the stipital sclerites. The spurs are not very distinct since only the tips are well sclerotized. Also, they are easily confused with the prominent posterior pleural processes. These latter structures, too, are exceptional in *M. maraisi*. The well-developed hypostomal spurs in *M. maraisi*, together with the presence of labial processes, have important implications in the placement of genera (notably *Zele* Curtis) in the Macrocentrinae (Čapek 1970; Nixon 1938; Short 1952). The most distinctive features of *M. maraisi* are the unmistakable labial processes and heavily-sclerotized stipital sclerites (fig. 48). *M. maraisi* larvae lie tightly against the sides and lower part of their cocoons until shortly before pupation (Marais 1955). The mouthparts face away from the cap end and can often be seen through the cocoon walls. Thus *M. maraisi* pupae and their hyperparasitoids, which both lie free in the cocoons, can be recognised at a glance.

The position of the hypostomal spurs in the agathidines is unclear. Čapek (1970) states they arise from the stipital sclerites while Short (1952) maintains they may arise from the hypostomae and appear to be lightly fused to the stipital sclerites. This is the most marked difference between *Cr. frustalis* (fig. 49)

and *Cremnops* (*Bracon*) *vulgaris* Cresson in which the spurs are attached to the stipital sclerites only (Simmonds 1974a). The elaborate epistoma and pleurostomae in *Cr. frustalis* are distinctive, as are the projections of the sides of the labial sclerites. Because *Cr. frustalis* is normally recovered from fifth-instar hosts the mouthparts are always relatively large.

Broodryk (1969) illustrates *Ch. curvimaculatus* larval mouthparts a little differently from fig. 50. The hypostomal spurs were found to be somewhat longer than illustrated by Broodryk, nearly reaching the stipital sclerites and shaped slightly differently. It is characteristic of the genus that the hypostomal spurs never reach the stipital sclerites (Short 1952). This is confusing in *Ch. curvimaculatus* for they are close together and sometimes appear to be actually touching. The shape of the spurs is also misleading. At low magnification only the more heavily sclerotized parts are visible and they appear as thin (but clear) lines, not as broad plates as figured. The most striking features of *Ch. curvimaculatus* are the distinct labial sclerites and equally distinct stipital sclerites which, moreover, curve slightly upwards.

Broodryk (1967) noted that in *T. picta* (fig. 47) the pleurostomae are weakly developed and difficult to locate. In live specimens they are especially difficult to see. However, the broken labial sclerites (which are characteristic of the Cremastini discussed by Short (1959), together with the curved hypostomae and stipital sclerites, make identification easy.

St. breviscapus (fig. 51) is the only ichneumonoid parasitoid of *L. frustalis* in which the blades of the mandibles are

the most prominent of the head sclerites. The rest are all weakly sclerotized and difficult to see. The maxillae are broad plates which overlie the bases of the mandibles and create an illusion of hypostomal spurs. The latter sclerites could not be located, but this is not in keeping with their known presence in other mesochorines (Short 1976). A thickening of the cuticle between the posterior pleurostomal processes and the stipital sclerites are shown as dotted lines in fig. 51. If these are in fact the hypostomal spurs, their location is unusual. *St. breviscapus* differs markedly in two ways from the *Stictopisthus* sp. figured by Short (1976): the mandibles curve downwards (contrary to others in the subfamily) and the labial sclerite is continuous.

The chalcids *Pr. rostratus* and *Pl. capensis* are easy to separate from each other and from the ichneumonoids. The undifferentiated maxillae and labia are characteristic of the chalcids (Short 1952). In *Pl. capensis* (fig. 52) the hypostomae, pleurostomae and lateral parts of the epistoma collectively form thin, distinct lines at low magnification. In *Pr. rostratus* (fig. 53) on the other hand, the mouthparts are practically impossible to see. The mandibular struts (Morris & Cameron 1935), which are extensions of the posterior pleurostomal processes, are not visible in live specimens of either species. A further distinction between the chalcids is the prominent thoracic and abdominal tubercles of *Pr. rostratus*, a characteristic of the genus (Parker 1924; Smith 1912; Tripp 1962).

KEY TO THE MOUTHPARTS OF MATURE LARVAE OF BOMBYLIID PARASITOIDS (FIGS 56 - 60)

1. Head ring continuous 3
2. Head ring discontinuous 4
3. Head ring broad (fig. 56) ..... *Geron* sp.
- Head ring narrow (fig. 57) ..... *Exhyalanthrax* spp.
4. Labrum conspicuous (figs 58 - 59) 'bombyliid sp.'
   Labrum inconspicuous (fig. 60) .. *Sp. incisurale*

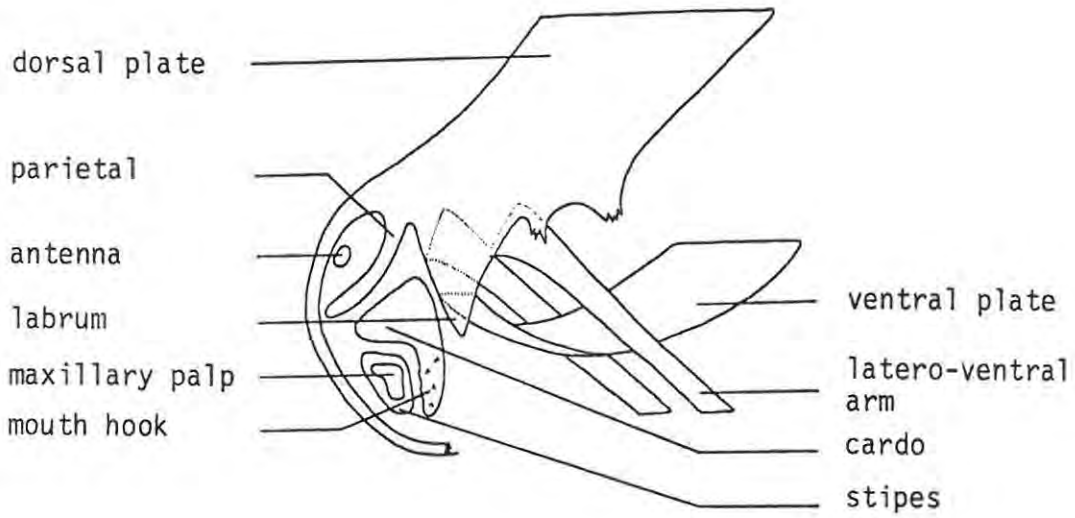
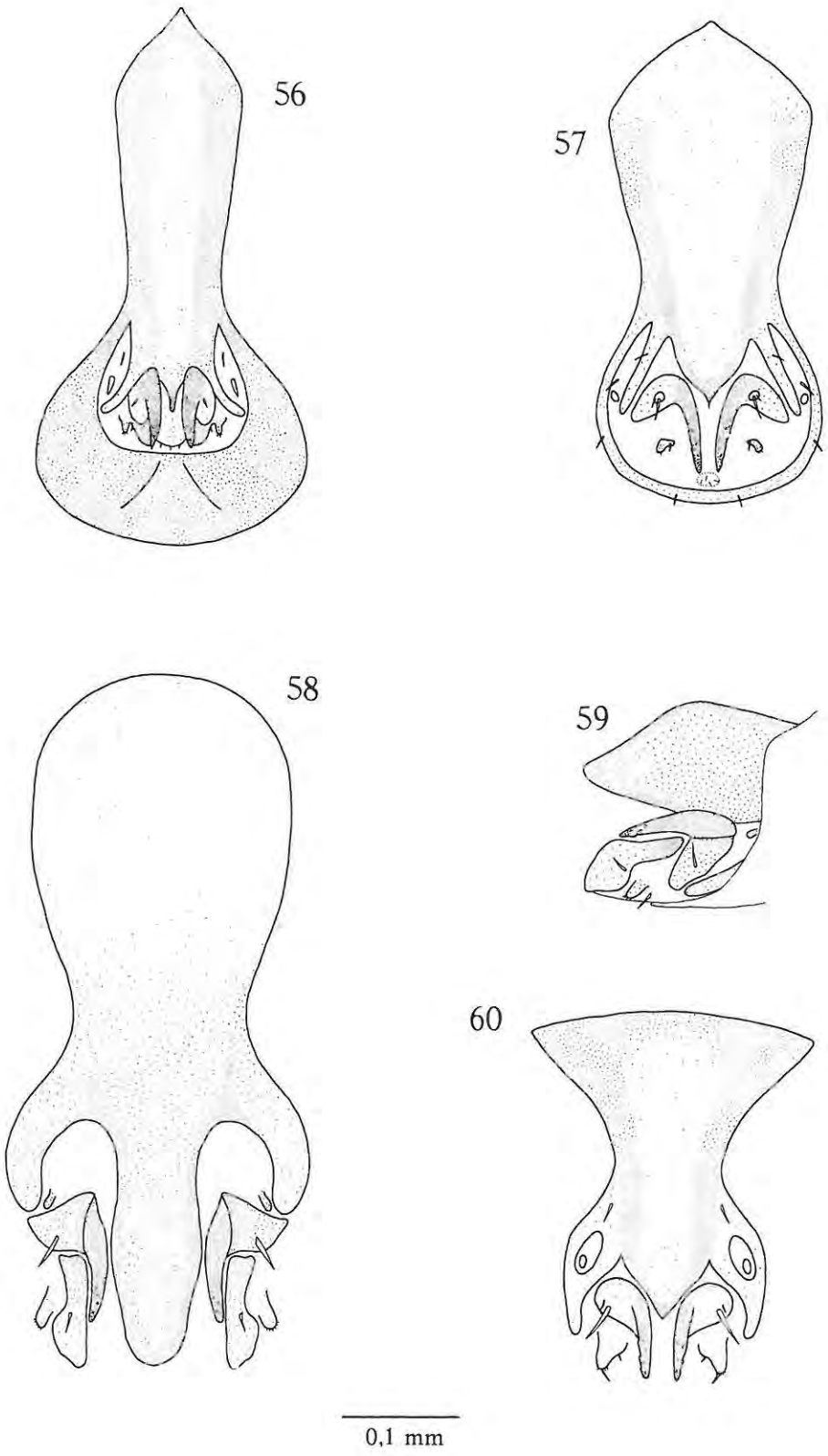


Fig. 55. A generalised diagram of the mouthparts of mature bombyliid larvae. Partly after Finlayson (1960).

The terminology of Berg (1940) and Brooks (1952) for the mouthparts and other head sclerites of mature bombyliid larvae is used (fig. 55). Only externally-visible structures are shown. The latero-ventral arms and ventral plates are located by dissection. The dorsal plates are partly obscured since the pharangeal skeleton (comprising the dorsal and ventral plates and latero-ventral arms) is withdrawn into the head and thoracic segments.



Figs 56 - 60. *L. frustalis* parasitoids. Head sclerites of mature bombyliid larvae, anterior and lateral aspects. 56. *Geron* sp. 57. *E. flammiger*. 58 - 59. 'Bombyliid sp.'. 60. *Sp. incisurale*.

The pharangeal skeleton is approximately perpendicular to most of the other structures (fig. 55). This structure is omitted from other illustrations, but the flat plane simplifies both interpretation and presentation. To recognise the various structures requires close examination under high magnification. Also, the mouthparts tend to be more compact than illustrated. If anything, the drawings exaggerate differences between the species and therefore require further comment.

The mouth-hooks are largely obscured by the well-developed stipites in the 'bombyliid sp.' (figs 58 - 59). In this species the beak-like labrum is very conspicuous compared to the other structures. In *Sp. incisurale* (fig. 60) and *Geron* sp. (fig. 56) the posterior parts of the dorsal plates are useful criteria; in the rest they are difficult to see. The sides of the dorsal plates tend to be more heavily sclerotized than the centres. This creates an illusion of separate sclerites converging towards the labrum. Together with the parietals they form inverted y's which are distinctive in the *Exhyalanthrax* spp. (fig. 57).

The head sclerites of *Geron* sp. (fig. 56) are difficult to interpret and not yet fully understood. A pair of heavily sclerotized, bifurcate arms (not illustrated) project backwards from the internal surface of the maxillary areas and appear to arise from the stipites. Sometimes they are externally visible as prominent bulbous structures adjacent to the tips of the mouth-hooks. A further structure, whose nature is obscure, lies between the mouth-hooks. The most characteristic part in *Geron* sp. is the conspicuous head-ring.

KEY TO THE SPIRACLES OF MATURE LARVAE
OF BOMBYLIID PARASITOIDS (FIGS 62 - 67)

1. Peritremes present 3
2. Peritremes lacking 4
3. Posterior and anterior spiracles
   with peritremes (figs 62 - 63) .... *Sp. incisurale*
\- Anterior spiracles without
   peritremes (figs 64 - 65) ..... *Geron* sp.
4. Spiracles with distinctly
   sclerotized structures (fig. 66) .. *Exhyalanthrax* spp.
\- Spiracles indistinct (fig. 67) ..... 'bombyliid sp.'

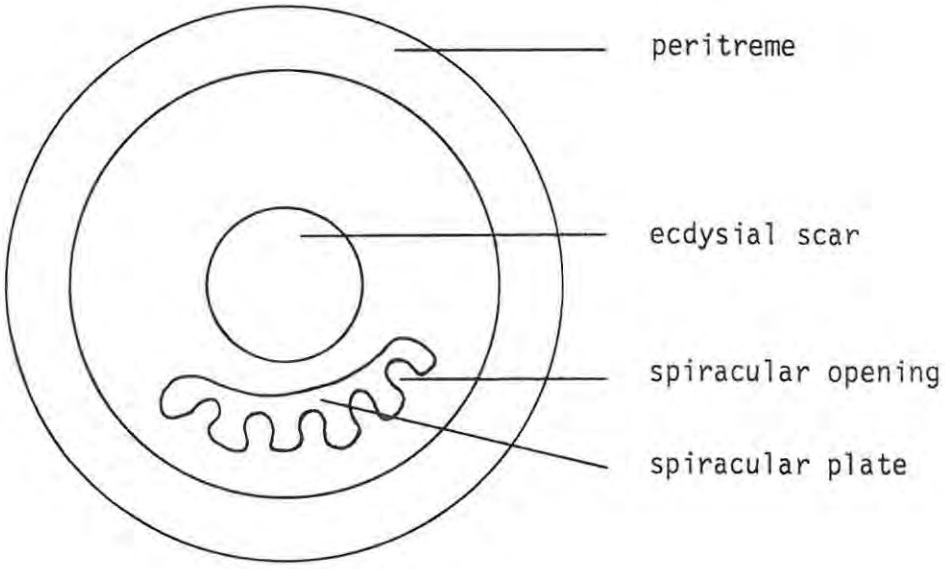
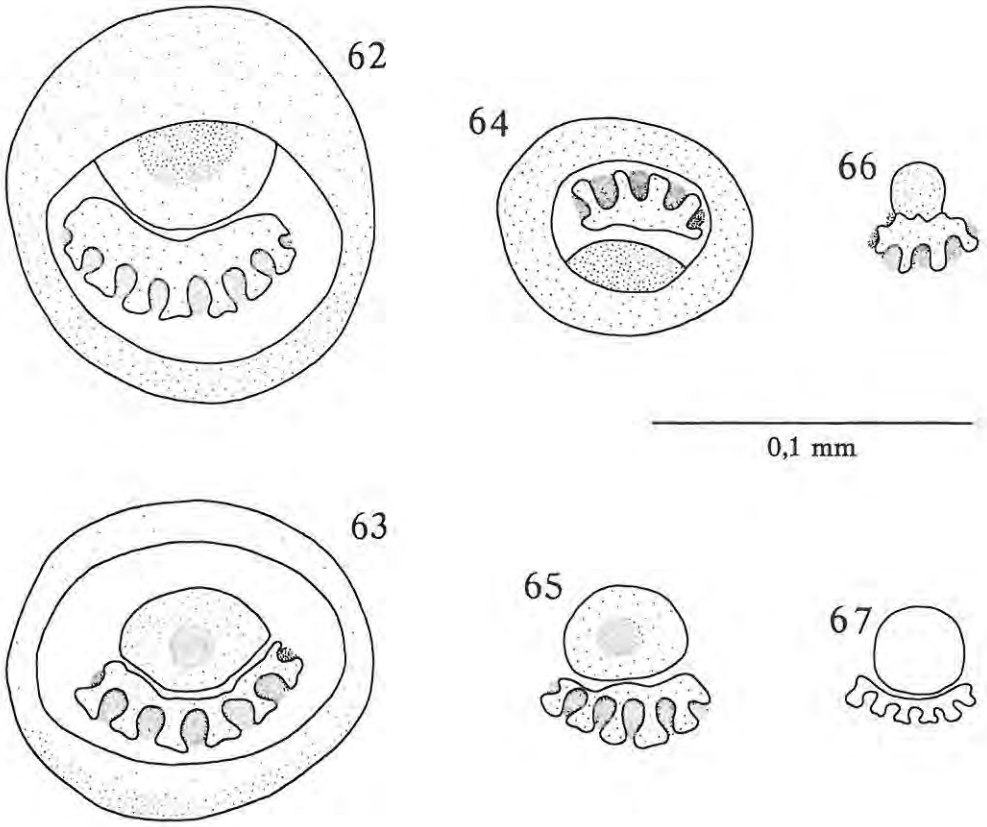


Fig. 61. A generalised diagram of the spiracles of mature bombyliid larvae. Partly after Keilin (1944).



Figs 62 - 67. *L. frustalis* parasitoids. Spiracles of mature bombyliid larvae. 62 - 63. *Sp. incisurale*. 62. Posterior. 63. Anterior. 64 - 65. *Geron* sp. 64. Posterior. 65. Anterior. 66. *E. flammiger* posterior. 67. 'bombyliid sp.' anterior.

Keilin (1944) states that dipterous larvae have eight abdominal segments while others agree that bombyliids have nine (Berg 1940; Brooks 1952; Hull 1973; Imms 1964). To avoid confusion the spiracles on the eighth abdominal segment are herein simply called posterior spiracles as opposed to the anterior (prothoracic) pair. Bombyliid larvae are amphipneustic (Hull 1973). In most of the species discussed here the spiracles are easy to locate. This is not so in the 'bombyliid sp.', in which clearly-sclerotized structures are lacking; for practical purposes the spiracles themselves may be considered absent. In this species the prominent mouthparts usually renders spiracle structure super-

fluous.

The spiracles are illustrated semi-diagrammatically in figs 62 - 67, following the terminology of Keilin (1944) (fig. 61). The papillae in the openings are not shown since they are indistinguishable, under low magnification, from the surrounding sclerotized areas of the felt chamber. The illustrations are in a flat plane. This hides the more-or-less raised nature of the spiracular plates, an outstanding feature of the posterior spiracles in *Geron* sp. (fig. 64). All the spiracles are of the Keilin Type III, that is where the spiracles of the earlier instars remain visible as an ecdysial scar. These lie to one side of the plates and are useful for locating spiracles. In *Geron* sp. (fig. 64) and *Sp. incisurale* (figs 62 - 63) the scars are partly obscured by overlying peritremes. Only those parts of the spiracular plates which carry the openings are illustrated. To indicate the boundaries between the spiracular plates of the various instars would require an unnecessarily detailed study.

The number of spiracular openings appears to vary within species and even between members of a pair of spiracles (Berg 1940; Brooks 1952). No significance must be attached to the numbers of spiracular openings figured. For *Exhyalanthrax* spp. (fig. 66) and the 'bombyliid sp.' (fig. 67) only posterior or anterior spiracles respectively are illustrated; no structural differences between the pairs were noted.

A few other characteristics of the bombyliid parasitoids of *L. frustalis*, apart from larval mouthparts and spiracles are useful for preliminary identifications. In *Sp. incisurale* the final larval exuviae are about the same shape as the larvae. The con-

dition has not been seen in 'bombyliid sp.'; in the others the exuviae collapse. Also in *Sp. incisurale*, the terminal abdominal segments are relatively small so that the tip of the abdomen has a 'stepped' appearance. In the 'bombyliid sp.' the integument is less transparent (virtually opaque so that internal organs cannot be seen in live larvae) than in the others. The venter of each thoracic segment carries a pair of prominent setae similar to those illustrated by Berg (1940).

So far, reliable criteria to separate the species of *Exhyalanthrax* have not been found. The cuticular armature of *E. lugens* appears to be the more prominent and while differences in these structures are valid criteria (Brooks 1952), they have not been developed for use here.

APPENDIX 6. The identification of pupae of *L. frustalis* parasitoids

It is rarely necessary to identify the HYMENOPTEROUS pupae. Healthy pupae are usually in a cocoon (their own or that of a host), with adult emergence imminent; both adults and cocoons are easier to recognise than pupae. Dead pupae also tend to be distorted. A few adult characters (Appendix 7) already manifest in pupae can be useful. These are the typical legs of chalcidids and the characteristic abdomens of *Ch. curvimaculatus*, *Pr. rostratus* and *St. breviscapus*.

The BOMBYLIID pupae, on the other hand, are unmistakable and are keyed below using the terminology of Hull (1973) which is illustrated in fig. 68. The anterior cephalic thorns are different in all the species, while the other characters distinguish the genera. No pupae of 'bombyliid sp.' have been found. The keys are elaborate in the hope that they can easily accommodate this species eventually. The branched nature of the hairs of *Geron* sp. (fig. 74) is exaggerated in the diagram but is nevertheless easy to see at low magnification.

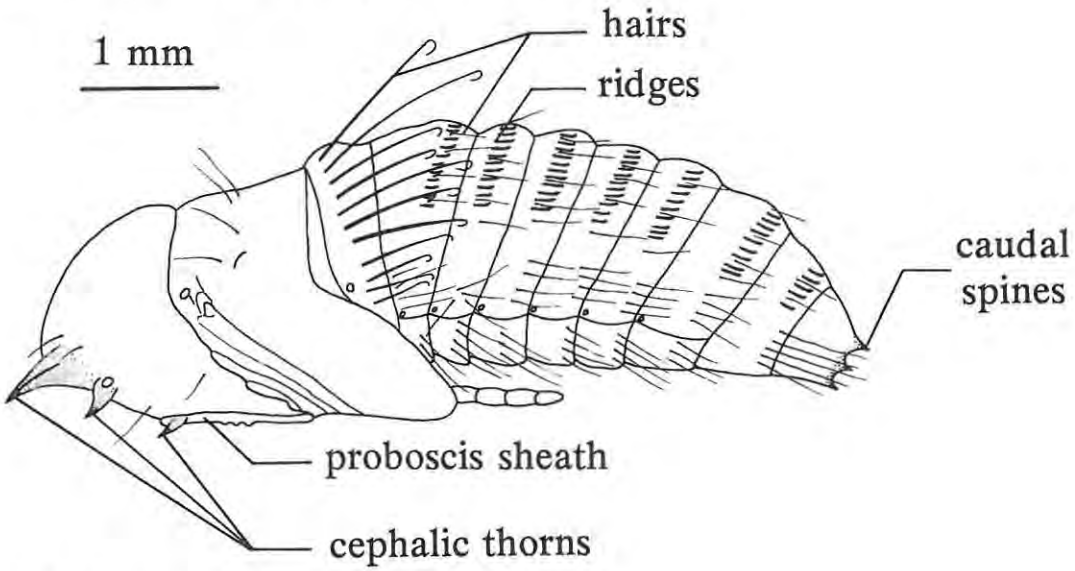


Fig. 68. *E. flammiger* pupa

KEY TO THE CEPHALIC STRUCTURES OF PUPAE OF BOMBYLIID PARASITOIDS (FIGS 69 - 72)

1. Antennal sheaths present; anterior thorns close-knit; median and posterior thorns lacking (fig. 69) ..... *Geron* sp.
- Antennal sheaths lacking; tips of anterior thorns widely separated; 3 pairs of thorns present 2
2. Anterior and median thorns fused into fan-shaped structure (fig. 70) ..... *Sp. incisurale*
- Anterior and median thorns separate 3
3. Anterior thorns v-shaped, tips sharp (fig. 71) ..... *E. flammiger*
- Anterior thorns u-shaped, tips broad (fig. 72) ..... *E. lugens*

KEY TO THE ABDOMINAL RIDGES AND HAIRS OF PUPAE OF BOMBYLIID PARASITOIDS (FIGS 73 - 75)

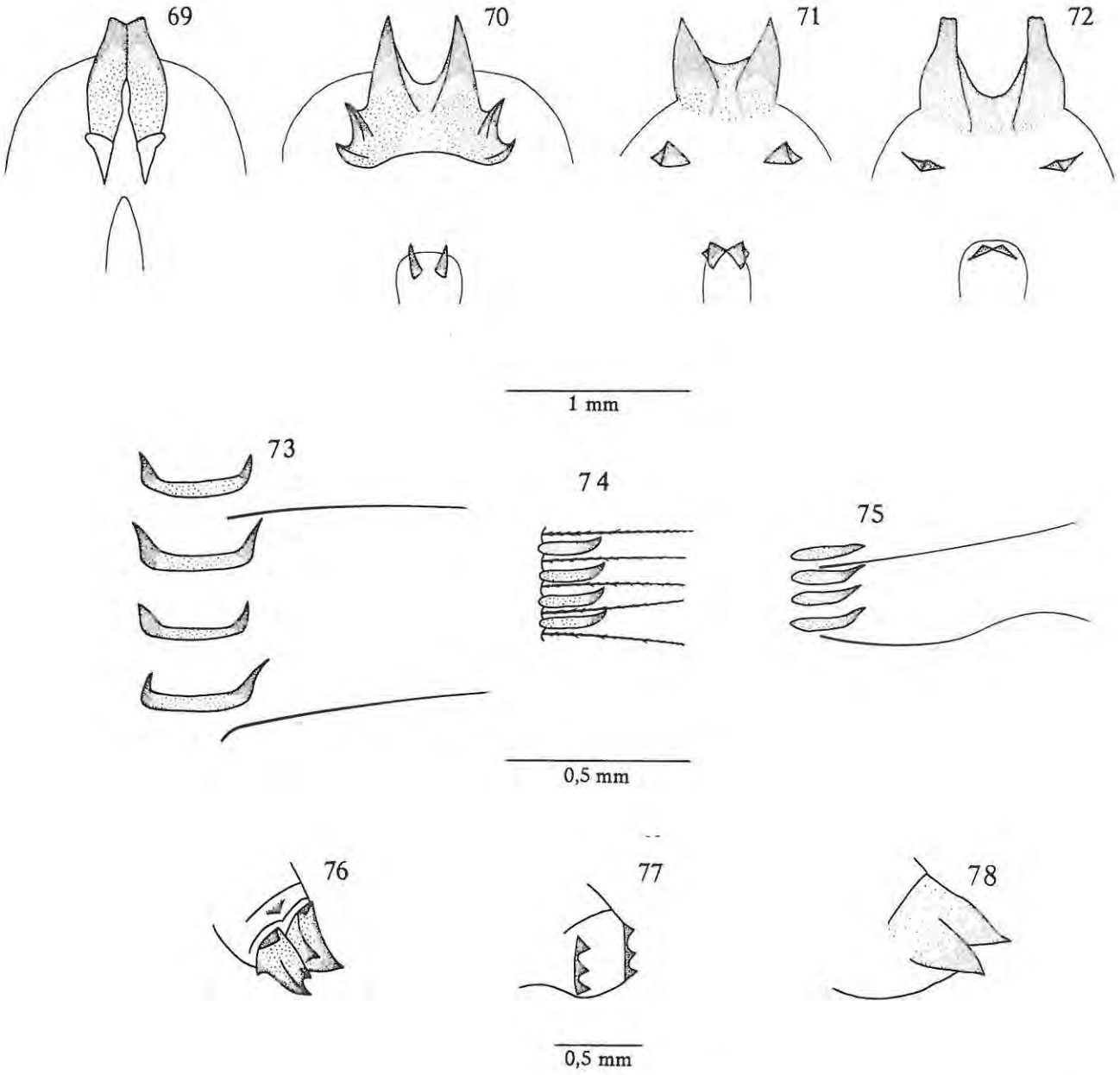
1. Anterior and posterior ends of ridges protrude (fig. 73) ..... *Sp. incisurale*
- Only posterior ends of ridges protrude 2
2. Hairs branched, alternate with ridges; impart comb-like appearance (fig. 74) ..... *Geron* sp.
- Hairs smooth, irregularly positioned in relation to ridges (fig. 75) ..... *Exhyalanthrax* spp.

KEY TO THE CAUDAL SPINES OF PUPAE OF BOMBYLIID PARASITOIDS (FIGS 76 - 78)

Multipronged (fig. 76) ..... *Sp. incisurale*

Single-pronged (fig. 77) ..... *Geron* sp.

3-pronged (fig. 78) ..... *Exhyalanthrax* spp.



Figs 69 - 78. *L. frustalis* parasitoids. Bombyliid pupae. 69 - 72. Cephalic thorns, postero-ventral aspects. 69. *Geron* sp. 70. *Sp. incisurale*. 71. *E. flammiger*. 72. *E. lugens*. 73 - 75. Abdominal ridges and hairs. 73. *Sp. incisurale*. 74. *Geron* sp. 75. *E. flammiger*. 76 - 78. Caudal spines. 76. *Sp. incisurale*. 77. *Geron* sp. 78. *E. flammiger*.

APPENDIX 7. The identification of adults of *L. frustalis* parasitoids

The adults of *L. frustalis* parasitoids all look very different. They have been the subject of several taxonomic studies (Annecke & Moran 1977) and specimens of all are in the National Collection of Insects in Pretoria.

KEY TO THE ADULTS OF HYMENOPTEROUS PARASITOIDS (FIGS 79 - 85)

1. Venation ichneumonoid, colour variable 3
2. Venation chalcidoid, colour mainly black 5
3. Wings smoky black; body reddish-orange (fig. 79) ..... *Cr. frustalis*

   Wings hyaline 4
4. Black with white band at base of abdomen (fig. 80) ..... *Ch. curvimaculatus*

\- Reddish-brown and black (fig. 81) .. *M. maraisi*

\- Black and yellow (fig. 82) ..... *T. picta*

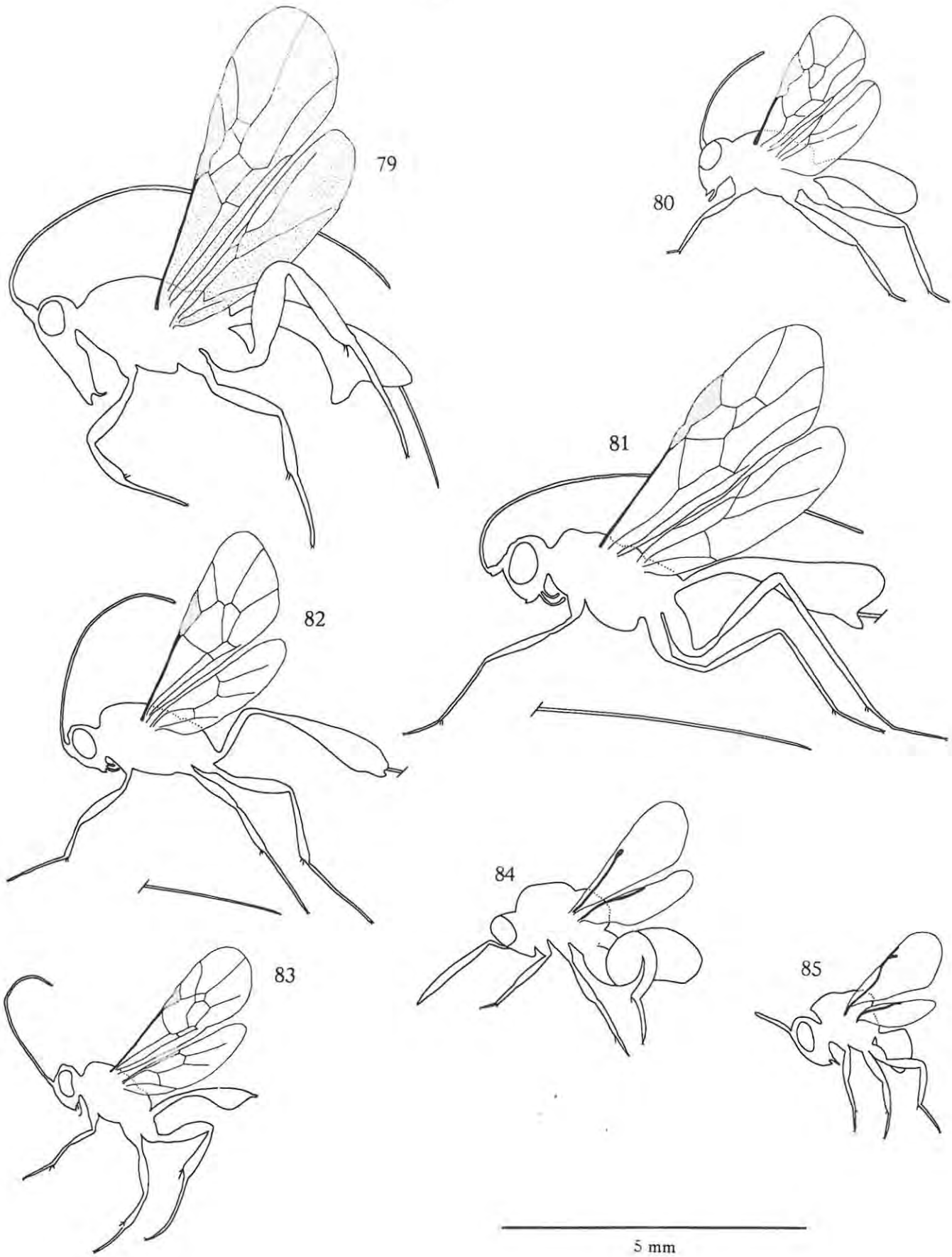
\- Pale yellow and brown (fig. 83) ... *St. breviscapus*

5. Gaster ovaliform; legs typical chalcidid (fig. 84) ..... *Pl. capensis*

\- Gaster triangulate (fig. 85) ..... *Pr. rostratus*

KEY TO THE ADULTS OF BOMBYLIID PARASITOIDS (FIGS 86 - 89)

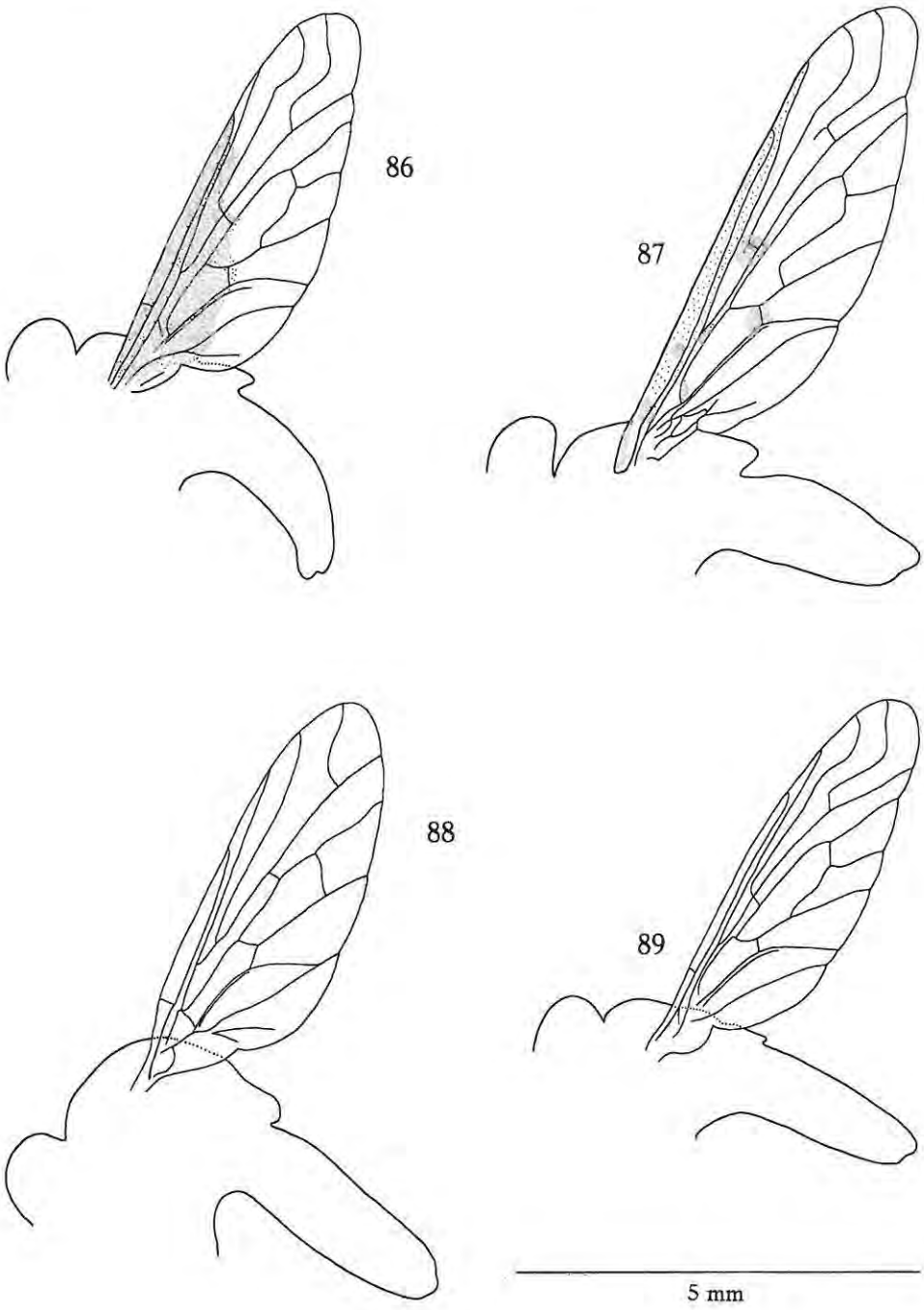
1. Wings marbled 3
2. Wings hyaline 4
3. Anterior part of wings evenly black (fig. 86) ..... *E. lugens*



Figs 79 - 85. *L. frustalis* parasitoids. Simplified outline diagrams of hymenopterous adults. 79. *Cr. frustalis*. 80. *Ch. curvimaculatus*. 81. *M. maraisi*. 82. *T. picta*. 83. *St. breviscapus*. 84. *Pl. capensis*. 85. *Pr. rostratus*.

- Wings spotted (fig. 87) ..... *Sp. incisurale*

4. Conspicuous silvery pubescence;
   thorax convex (fig. 88) ..... *Geron* sp.
- Pubescence and setae impart a striped
   appearance; thorax flat (fig. 89) .. *E. flammiger*



Figs 86 - 89. *L. frustalis* parasitoids. Simplified outline diagrams of bombyliid adults. 86. *E. lugens*. 87. *Sp. incisurale*. 88. *Geron* sp. 89. *E. flammiger*.

APPENDIX 8. The identification of cocoons of *L. frustalis* parasitoids

KEY TO THE COCOONS OF HYMENOPTEROUS PARASITOIDS (FIG. 90)

1. Dark; with saucer-shaped cap; thickening around middle lacking .... *M. maraisi*

\- Light; cap lacking; thickening variable 2

2. Dull whitish-grey; stout; distinct thickened band around middle ..... *T. picta*

\- Shiny silvery; stout; band usually lacking, at most faint ..... *Ch. curvimaculatus*

\- Shiny silvery; flimsy; band lacking but with thickening in one or a few spots ..... *Cr. frustalis*

1 cm

Fig. 90. *L. frustalis* parasitoids. Cocoons. Clockwise from top left: *M. maraisi* (weathered), *M. maraisi* (fresh), *T. picta* (weathered), *T. picta* (fresh), *Ch. curvimaculatus* (fresh), *Cr. frustalis* (fresh).

Table 17. Characteristics of the cocoons of *L. frustalis* parasitoids.

Characteristic	Parasitoid			
	Ch. curvimaculatus	*Cr. frustalis*	*M. maraisi*	*T. plet*
Size variation	Slight	Slight	Considerable	Considerable
Shape	Barrel, rarely cylindrical	Oval	Oval	Oval
Cap present	No	No	Yes. About 0,1 of total length	No
Thickening	Sometimes faint band around middle on inner surface	In one or few spots	Inner surface of saucer-shaped cap with loose, coarse brown strands and thin amber discs	Conspicuous white band around middle on inner surface
Transparent	No	Yes	Slightly, especially when fresh	No
Principal layers	Two: outer loosely woven; inner thin, multilayered, smooth, closely woven	One: inner surface smoother than outer	Three: outer flimsy except tip of cap; middle stout, parchment-like; inner stout, pliable, probably secreted (see Gadd (1946)). Middle and inner multi-layered, smooth. Outer and middle continuous with cap; inner discontinuous, both ends closed	Two: outer loosely woven, continuous, denser at ends and middle; inner multi-layered, smooth, closely woven
Principal layers easily separated	No	Only one layer	Yes, especially inner two	No
Structure	Average	Flimsy	Stout	Average
Colour (fresh)	Shiny silver	Shiny silvery-white	Shiny brown, imparted by middle layer; inner layer amber; outer layer white, prominent in tip of cap	Dull greyish-white, imparted by outer layer; inner layer shiny silvery-white, band paler than rest
Colour (weathered)	Dull or shiny pale yellow	Off-white	Shiny dark brown, imparted by middle layer; outer layer brown, darker than outer, tip of cap darkest; inner layer unchanged	Dullish brown; band paler than rest, stains inner layer
Position in host larval case	Lower end. Shiny mark where joined to host case	Lower part	Lower end. Shiny mark where attached to host case	Lower part
Position of host remains	Usually between lower end of cocoon and host case	?	Cap end of cocoon, shape of host remains characteristic	Variable
Position of emergence hole	Near top	Near top	Cap removed, usually hinged to cocoon	Near top

Of the *L. frustalis* parasitoids, only the primary hymenopterans construct cocoons. Normally the cocoons can be identified at a glance, but to allow for special situations (such as when the material is weathered) additional characteristics are recorded in Table 17. Captive *M. maraisi* larvae abort cocoon construction when not held in a host larval case or a close facsimili. This leads to loose bundles of pale yellow silk or, more rarely, flimsy white to yellow cocoons without a cap. Such larvae always die. Otherwise, aborted cocoons have been noted only in *Ch. curvimaculatus*. The silvery colour of the silk is still evident and distinct from that of *M. maraisi* and the larvae usually survive.

The white outer layer in freshly-spun *M. maraisi* cocoons is useful in identification. Because the mature larvae undergo arrested development there are no other indications of the age of cocoons.

APPENDIX 9. The identification of *L. frustalis* pathogens

The white mycelial growth and spores of *Beauveria bassiana* are unmistakable (fig. 91) - hence the common name 'white muscardine' - and are illustrated by several authors (e.g. Andreadis 1980; Steinhaus 1964; Timonin *et al.* 1980). When the fungus kills *L. frustalis* larvae but fails to sporulate, the 'mummies' are hard, brittle and a characteristic brown colour.

1 cm

Fig. 91. *L. frustalis* encased larvae killed by *B. bassiana*.

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