Important Biological and Ecological Aspects of *Strepsicrates macropetana* Meyrick (Lepidoptera: Tortricidae)

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Abstract

Strepsicrates macropetana Meyrick (Tortricidae) has a significant impact on eucalypt form and growth, therefore is an important insect pest of young plantations in New Zealand. The current research was undertaken to provide essential information regarding the biology, behaviour, phenology and chemical ecology of *S. macropetana*. All experiments were conducted within laboratories and/or glasshouses located at Massey University, Palmerston North, during the 1998/1999 period. The use of a cage containing eucalypt foliage enabled an efficient, self-maintaining method of rearing.

A full life-cycle of *S. macropetana* was completed within approximately 54 days. Female *S. macropetana* had an average fecundity of 40 eggs, with an egg to adult survival rate of 62.5%. The eucalypt species on which the larva developed on had an effect on the growth of *S. macropetana*. However, no one host species achieved optimal growth on all parameters. When given a choice between eucalypt and non-host (apple) foliage, *S. macropetana* females oviposited more eggs on the eucalypt foliage, depositing significantly more on the lower surface of the leaf, predominately around the central mid-vein region.

Between four and five generations of *S. macropetana* were identified in the field during a 12-month period. The abundance of *S. macropetana* was shown to be related to the larval host, and temperature. A significant relationship was also identified between pupal weight and these factors. The predominant natural enemy of *S. macropetana* in the field was identified as *Trigonospila brevifacies* (Hardy) (Tachinidae), in which larval parasitism rates of up to 45% were found.

Sexual activity was predominant within the first and second hours of the scotophase, reaching a maximum when adults were three to five days old. Oviposition behaviour was most frequent around the second, fifth and seventh hours of the scotophase, peaking when adults were six to eight days old. Egg viability declined as female age increased, from 55% viability on day seven down to 31% on day nine. Male *S. macropetana* were shown to be attracted to female *S. macropetana* in a Y-tube assay. Biologically active compounds were isolated from female *S. macropetana*, and the main compound was preliminarily identified as (*E*)-7-Dodecenyl acetate. This, in addition to moderate amounts of other compounds are likely to constitute the sex pheromone of *S. macropetana*.

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1. Introduction

1.1 *Strepsicrates macropetana*

Strepsicrates macropetana Meyrick, commonly referred to as the *Eucalyptus* leafroller, is a tortricid pest of eucalypts in both Australia and New Zealand (Elliott *et al.* 1998). As a typical tortricid, *S. macropetana* has a phytophagous larval stage prolific under large-scale monoculture conditions.

The larvae of *S. macropetana* commonly feed on the inflorescence, shoot tips, young leaves, buds and developing flowers of young *Eucalyptus* trees (Fig. 1), and are occasionally observed feeding on mature trees (Kay 1991). The foliage is typically webbed with silken threads to form a protective leaf shelter in which the larva resides, feeding on the plant tissue within (Nuttall 1983). Consequently the leaves become skeletonised, eventually browning and dying prematurely (Fig. 2). The larva will vacate and construct additional shelters, building several within its lifespan. The shelters take on a variety of appearances, the most common being when two or three leaves are webbed together, side by side.

Fig. 1. Damage resulting from *Strepsicrates macropetana* (left).

Fig. 2. Damage to *Eucalyptus* leaves.

The feeding habits of *S. macropetana* can severely limit the growth potential of young *Eucalyptus* trees. The damaged shoot growth can stunt tree development, resulting in malformations such as multi-leadering (T. Withers, pers. comm.). Damage to buds and fruit capsules can furthermore, reduce the seed production of the tree (Zondag 1979). Overall, the negative impact is likely to be considerable on young eucalypt plantations, nursery stock and seedlings in Australia and New Zealand, even though no research has directly quantified the effect.

1.2 Taxonomy

- Phylum Arthropoda
- Class Insecta
- Order Lepidoptera
- Family Tortricidae
- Sub-family Olethreutinae
- Tribe Eucosmini
- Genus *Strepsicrates*

Strepsicrates macropetana is a defoliator from the family Tortricidae. This cosmopolitan family includes over 5000 species, still with a large number to be recorded, making it one of the largest families of microlepidoptera (Horak & Brown 1991). The subfamily Olethreutinae comprises over 3190 species, 335 genera within 6 tribes (Horak & Brown 1991). The genus *Strepsicrates* was preoccupied as *Strepsiceros* Meyrick in 1881 and *Strepsiceros* Smith in 1827 (Meyrick 1881). The genus was revised in 1911 and most species were put in the European genus *Spilonota* Stephens 1829. However, the concept of *Strepsicrates* was eventually restored by Dugdale (1988). The genus *Strepsicrates* is characterised by a smooth thorax; a deep notch in the antennae of the male; veins seven and eight of the fore wings are separate; and veins three and four of the hind wings are long-stalked (Meyrick 1881). The genus is widely distributed and extensively represented in Australia, also occurring in New Zealand, other countries within the commonwealth, and the Oriental and Pacific regions (Dakshinamurthy & Bhandarkar 1986; Ahmad 1974; Braza 1991).

Strepsicrates macropetana was first described from Blackheath, New South Wales, Australia, by E. Meyrick between 1879 and 1887 (J. Dugdale, pers. comm.), from which the first and only detailed description of the insect was given (Meyrick 1881). It has been recorded in New Zealand since the early 1920's (Philpott 1923), present before the introduction of effective forestry quarantine in 1948 (Forest Health 1993). The first record of *S. macropetana* was within the Auckland region in 1921 (Dugdale 1988).

1.3 Pest status

Strepsicrates macropetana is native to Australia, occasionally reaching pest status in some locations, e.g. Brisbane and Canberra (M. Steinbauer, pers. comm.). As documented by Philpott (1923), it is widely distributed throughout Australia, having been recorded in Queensland, Victoria, New South Wales, South Australia and Western Australia. This insect has not been regarded as a major pest in other parts of Australia, due in part to the presence of *Strepsicrates semicanella* (Walker), which occupies a similar ecological niche (R. Wylie, pers. comm.). *Strepsicrates semicanella* has never been recorded within New Zealand eucalypt plantations (W. Faulds, pers. comm.).

During the decades that followed its' discovery in New Zealand, *S. macropetana* was not regarded as a significant insect pest, due to the negligible amount of *Eucalyptus* grown at the time. However by the 1970's, the depletion of indigenous *Podocarpus* species and native tawa (*Bielschmedia* species) forests became evident (Barr 1996), and the botany and timber properties of most *Eucalyptus* species were recognised, resulting in a renewed interest for growing eucalypts. The *Eucalyptus* species grown today are the result of intensive research and are lucrative for a variety of purposes including soil conservation, decorative timbers, furniture, veneer, firewood, wind-shelter and for pulp and paper (Hathway & King 1988; Lembke 1977; Barr 1996). The area of hardwood planted within New Zealand has increased by 47% in the last ten years (NZ Forest Stats 1998), of which eucalypts account for almost 50% of the area planted (NZFOA 1997). However, forestry in New Zealand is still dominated by soft wood production, i.e. *Pinus radiata* D. Don, with hardwoods only accounting for around three percent of the total plantation forestry estate (NZFOA 1997).

The recent increase in eucalypt plantations grown in New Zealand has resulted in an increased distribution of *S. macropetana*. Currently, *S. macropetana* has a distribution throughout the country, from Auckland to Southland (Dugdale 1988). It has been recorded on at least fifteen *Eucalyptus* species within the subgenera *Symphyomyrtus* and *Monocalyptus*. These included *E. botryoides* J. Sm., *E. fastigata* Deane et Maiden, *E. nitens* (Deane et Maiden) Maiden, *E. obliqua* L' Herit, *E. regnans* F. Muell., and *E. saligna* J. Sm. (Nuttall 1983).

1.4 Current control

The management of insect pests under nursery conditions is critical for future growth prospects of young *Eucalyptus* trees (Kay 1991). Therefore, seedling stock is usually protected from insect pests by regular insecticidal sprays. Many *Eucalyptus* pests are now controlled or selected against by a variety of improved forestry practises including the cautious use of eucalypt species, improved forest hygiene, and knowledge of the pest species and their biological control agents (Forest Health 1993). For example, the *Eucalyptus* tortoise beetle (*Paropsis charybdis* Stål) was a primary pest of *Eucalyptus* and is now effectively controlled by the egg parasite *Enoggera nassaui* (Girault) (Kay 1990). Biological control agents also manage other insect pests occurring in *Eucalyptus* plantations, e.g. *Phylacteophaga froggatti* Riek. According to Nuttall (1983), an unidentified protozoan and other natural enemies have contributed to the regulation of *S. macropetana* in the past.

The use of insecticidal sprays has been commonly instigated during severe outbreaks against *Eucalyptus* pests, such as *P. charybdis, Eriococcus coriaceus* Maskell and *Cardiaspina fiscella* Taylor. Insecticides are not, however, a viable method for controlling *S. macropetana* due to its protected niche and an insufficient knowledge of phenology used to determine optimal spraying times. Currently, no control method is implemented against *S. macropetana* in a *Eucalyptus* plantation situation. This is not because control is deemed unnecessary but no effective method exists.

1.5 Aims and objectives

Based on forest health observations, it was evident that *S. macropetana* posed a potential risk to young *Eucalyptus* plantations. Given the lack of feasible management options it was decided that biological and ecological research of *S. macropetana* was required to aid in the development and instigation of alternative pest management methods in the future.

Fundamental information such as instar determination, development time and fecundity had not been determined for *S. macropetana* prior to this study. Therefore, the primary goal was to provide a reliable foundation concerning the life history of *S. macropetana*. From this basis, more detailed investigation into the reproductive and host selection behaviour, phenology, and pheromone biology of *S. macropetana* was possible. The following objectives were formulated for this study:

1. To develop and maintain a laboratory colony of *S. macropetana*.

2. To investigate the life history and biological parameters of *S. macropetana*.

3. To investigate the natural phenology and abundance of *S. macropetana*.

4. To investigate the reproductive and host plant selection behaviour of *S. macropetana*.

5. To identify the general nature of the female sex pheromone of *S. macropetana*.

2. Literature Review

2.1 Exotic forestry in New Zealand

Planting of exotic tree species has been a part of New Zealand heritage for many decades. The establishment of fast growing exotics boomed during the 1960s and 1970s, giving rise to the beginning of production plantation forestry within New Zealand (Forest Health 1993). Various local and export markets have become reliant on the industry, resulting in a current plantation estate of 1.3 million hectares. Approximately 1.1 million hectares have been planted in *Pinus radiata*, where 70% are less than fifteen years old. With the current rate of planting, it is estimated by the year 2010, four million hectares of exotic forest will exist (Forest Health 1993).

The extensive planting of radiata pine throughout New Zealand is due to its' fast growing ability, amenability to a wide range of conditions, and the continuous enhancements to improve growth, form and resistance (Forest Health 1993). Perturbation in market trends and unpredictable environmental conditions may have severe consequences for an industry based on a single species (monoculture). It is also widely acknowledged that such an environment is more susceptible to the outbreak of pests and diseases. Due to their narrow genetic base, Boyce (1954), Gibson and Jones (1977), and Ciesla and Donaubauer (1994) concluded monocultures to be of high risk. However, alternative viewpoints have also been expressed (Chou 1981; Bain 1981).

Investigation into complementary plantation species for New Zealand was instigated when the former New Zealand Forest Service (NZFS) selected nine exotic tree species for further evaluation as "special-purpose-species". This included several species from the genus *Eucalyptus* L'Herit (Myrtaceae) (Nicholas & Hay 1990). Eucalypts grow in a wide range of habitats, having excellent pulp and timber properties and rapid growth rates. Approximately twenty eucalypt species are commercially grown in at least fifty countries throughout the world (Ohmart & Edwards 1991). A wide range of eucalypts were initially planted in New Zealand. Weston (1957) reported that over one hundred eucalypt species had been planted, of which many have proven unsuitable for plantations purposes. Difficulties included site suitability, frost resistance, and insect and disease resistance (Fry 1983). Currently four species account for 90% of the total hardwood plantation area throughout New Zealand;

E. nitens, *E. fastigata*, *E. saligna* and *E. regnans*. There has been a renewed interest in growing plantation *Eucalyptus* in New Zealand for hardwood pulp, durable timber, shelter, and firewood. In accordance with Fry (1983) eucalypts account for less than 1.5% of the total exotic plantation estate within New Zealand. By 1998 approximately 46 000 ha of exotic hardwoods had been planted in New Zealand, of which we can assume at least 90% are eucalypts (NZFOA 1999), and it is likely that this will increase in the future.

Exotic phytophages pose a threat to the success of the *Eucalyptus* industry in New Zealand, as the chance of invasion by Australian insect species is pronounced due to the close proximity of Australia and the favourablity of New Zealand's climate. In addition, New Zealand has a paucity of exotic invertebrate fauna (Atkinson & Cameron 1993), therefore a relatively vacant niche exists for invading pest species. By 1991, 21 eucalypt insect pests from Australia had become established in other countries, of which 18 were in New Zealand (Ohmart & Edwards 1991). To date 57 phytophagous insect species of Australian origin have become established in New Zealand which have the potential to significantly impact on the health of eucalypts (T. Withers, unpublished data.). In the last ten years, eucalypts in New Zealand have had severe infestation problems with some of these Australian insects, particularly *Gonipterus scutellatus* Gyllenhal, *Eriococcus coriaceus*, *Phylacteophaga froggatti*, *Cardiaspina fiscella*, *Paropsis charybdis* and *Strepsicrates macropetana* (Forest Health 1993). *Strepsicrates macropetana* was previously regarded as insignificant but has recently become of increasing importance in young plantations of a number of eucalypt species (T. Withers, pers. comm.). Most of these pests have warranted control, therefore, biological control and eradication programs have been instigated (e.g. Bain 1977; Zondag 1977; Elliott *et al.* 1998). Before biological control, or other types of integrated management can be devised for *S. macropetana*, a greater understanding of the biology, phenology and chemical ecology of this species is required. This forms the basis for the current study.

2.2 Insect pest management

Since the mid 1900's, there has been an increasing concern related to the reliance and over-use of conventional pesticides (Carson 1962). The manifestation of chemical dependence has initiated the development of ecologically based alternatives to manage insect populations. Methods, such as the use of microbial pesticides, semiochemicals

(pheromones, kariomones, allomones), biological control and pesticides containing natural products are now accepted as some of the most rational means of insect control, through which appropriate control combinations have been designed to maximise the effect on the target species and minimise the disruption of beneficial species (Howse *et al.* 1998).

With the progression of pheromonal science, the identification of sex pheromone components and the production of synthetic pheromone analogues have become possible. Pheromones are highly selective, active in minute quantities, present minimal risk to non-target organisms and the environment, and have low potential costs of development. As a result many insect pest management techniques have been developed that utilise synthetic sex pheromones, including monitoring, mass trapping, lure and kill, and mating disruption (e.g. Doane *et al.* 1982; Bartell 1982). Various additional strategies exist which utilise pheromones. These include the use of deterrent pheromones, anti-aggregation and oviposition-deterring pheromones, stimulo-deterrent diversionary strategies and push-pull strategies (Howse *et al.* 1998; Foster & Harris 1997). The successful use of pheromones has contributed to a reduction in the use of pesticides. Howse *et al.* (1998) estimated in Ontario, Canada a 25% reduction in pesticide use has occurred, where 90% of apple growers now use integrated pest management strategies. The knowledge of pheromone function and chemistry is developing progressively, providing the basis for highly selective techniques of insect management. In New Zealand, pheromone traps have been successfully utilised, particularly for the identification of optimal spraying times, thus reducing inefficient and poorly timed pesticide application. Pheromone traps are generally cost effective; highly selective; require no insect sorting; and are sensitive at low population levels (Peet 1997). Traps have been successfully utilised to schedule spraying against various tortricid pests including *Epiphyas postvittana* Walker, *Planotortrix octo* (Dugdale) and *Ctenopseustis obliquana* (Walker) within New Zealand orchards (Tomkins *et al.* 1991b; Shaw *et al.* 1993; McLaren & Suckling 1993).

Tortricid management is currently pursued with a variety of control measures throughout different countries, many of which have been used individually or in combination for management programs. For example, management of the tortricid *Cydia molesta* (Busck) has been achieved with use of insecticides, food lures, sex

pheromones, biological control agents and cultural control methods (Rothschild & Vickers 1991).

The emphases for managing insect species in the future will most likely include the following (Howse *et al.* 1998).

- Expanding information gathering and processing activities on past and present populations.
- Combination and utilisation of more innovative resources such as genetically modified plants, pheromonal lures, biological and hormone-based pest control, and computerised decision-making aids.
- Increasing ability to make site-specific decisions that reflect the dynamic nature of a crop and its pests.
- Amelioration of pest resistance to pesticides.
- Expansion of integrated pest management (IPM) goals for social welfare and environmental sustainability on both the farm and beyond.
- Enrolment of the non-farming community in encouraging and rewarding IPM practice adoption.

Ecologically based methods are unique in their action comparative to pesticide based control methods, therefore, effective implementation requires a better understanding of insect biology and ecology by those who apply them. It is now evident that such methods will play an increasing role in pest management in the future.

2.3 Importance and distribution of tortricids

The family Tortricidae pose a considerable threat to land based industry throughout most parts of the world. Tortricids are destructive and difficult to control throughout the temperate climatic zones, and subsequently result in considerable economic losses in these areas (van der Geest & Evenhuis 1991). The economic impact of this family has been recognised particularly within the agricultural, horticultural and forestry sectors.

Tortricids have a phytophagous larval feeding stage, responsible for direct and indirect damage to numerous crops. Such damage can affect the growth, quality, yield and marketability of the final product. *Cydia pomonella* (L.) is a primary pest of stone and pome fruit, and occurs throughout Europe, North and South America, South Africa, Australia and New Zealand. Internal feeding results in direct damage to the fruit, with

infestation levels ranging from less than 15% to over 75%, dependent on the cultivars grown and habitat conditions (Barnes 1991). The cosmopolitan pest, *C. molesta* is also an internal feeder, with infestation rates on stone fruit ranging from 10% (Helson 1939) to 70% (Dustan 1960) (cited in Rothschild & Vickers 1991). *Epiphyas postvittana* has been recorded on over 250 plant species throughout Australia and New Zealand (Dugdale & Crosby 1995), where the percentage of produce damaged can exceed 30% and 50%, respectively, on unsprayed crops (Wearing *et al.* 1991). Tortricids associated with plantation forestry readily reach pest status. The most important forestry pests of this family in New Zealand include *Epiphyas postvittana*, *Ctenopseustis obliquana*, *Planotortrix notophaea* (Turner) and *Strepsicrates macropetana* (Kay 1991).

Damage caused by tortricid forest pests has had and will continue to have enormous economic implications. As reported by Milne (1986), *Choristoneura fumiferana* (Clemens) has had a substantial impact on the softwood production in Canada causing an estimate of $650 million in production loss between 1971 and the early 1980's, and a further $1.4 billion cost in forest rehabilitation. Further implications of *C. fumiferana* damage can be seen as potential unemployment in the forestry industry, reduced recreational value of the forest, and concerns about forest succession (Milne 1991).

With the current patterns of insecticide usage and the stringent international quarantine standards imposed, the presence of tortricid pests pose a significant problem to exporters and importers of natural commodities. Unless ecologically based and/or alternative control measures are pursued, the potential impact of tortricids on the agricultural, horticultural and forest industries will be colossal.

2.4 Rearing of tortricids

Most entomological research requires the establishment of rearing colonies. The success of a colony is attributed to obtaining the largest number of insects possible, whilst attaining long-term quality and performance of the insects within the shortest possible time frame. The terms adaptation, domestication and acclimatisation have been used to describe the biological processes observed throughout the laboratory establishment of an insect species (Ochieng'-Odero & Singh 1992). For these processes to be optimal, methodology must account for the specific requirements of the species reared.

2.4.1 Historical overview of rearing

Insect rearing has been practiced for many years, with the origin dating between 7000 B.C. to A.D. 1900. As reported by Singh and Moore (1985), the silk worm, *Bombyx mori* (L.), was recognised as the first insect to be reared by humans, dating back to 7000 years before present. Between 32 B.C. to A.D. 1578, a number of insect species were reared for medicinal purposes (Singh & Moore 1985), many of which are still reared today. Rearing in the twentieth century was revolutionised when Bogdanow (1908) developed an artificial diet for the blowfly, *Calliphora vomitoria* (L.) (cited in Singh & Moore 1985). A further advancement was the development of mass rearing for sterile male releases, during the pest management program against the screwworm, *Cochyliomyia hominivorax* (Coquerel), in 1936. Since then at least ten million flies have been released in Mexico and Texas (Singh & Moore 1985). With the progress of modern science, many insects are now reared under laboratory conditions, for subsequent use in research and pest management programmes. The current status of rearing is well documented by various authors including King and Leppla (1984) and Singh (1984). According to Singh (1985), approximately 92 tortricid species have been reared successfully. Singh (1977) and Singh and Moore (1985) present a compilation of successful methods for rearing various insect species, including diet recipes, containerisation and an overview of the basic life history parameters obtained.

2.4.2 Tortricid rearing

The rearing of an insect, with particular reference to tortricids, can be divided into four main stages, including egg handling, larval rearing, pupal collection, and adult handling, where quality control governs all stages (details found in Singh & Moore 1985; Singh *et al.* 1985).

In a typical tortricid program eggs are oviposited onto polythene or paper towelling sheets (Ochieng'-Odero & Singh 1992; Singh *et al.* 1985; Howell 1981). Sheets are replaced daily and held in paper lined petri dishes or plastic containers to regulate humidity. The eggs are cleaned with either a formaldehyde vapour or solution, and held at the appropriate temperature for development (Singh *et al.* 1985). Tortricids are most commonly reared with a photoperiod of between 16-18 light hours and 6-8 hours dark; a temperature between 18-24°C; and relative humidity between 60-70% (Singh *et al.* 1985). The larvae are individually reared in plastic test tubes or together in ventilated plastic containers (Singh *et al.* 1985). Eggs or neonate larvae are inoculated

onto conditioned diet and collected as pupae. The diets commonly used for tortricid rearing include the Singh (1983) diet and the Ivaldi-Sender diet (cited in Bathon *et al.* 1991). Pupation typically occurs at the top of the test tubes or on any rough substrate introduced (e.g. cardboard) (Clare *et al.* 1987). Harvested pupae are stored in petri dishes and maintained under the appropriate conditions.

Tortricids usually require conditions between 15-22°C and 50-60% relative humidity for successful mating to occur (Ochieng'-Odero & Singh 1992; Tomkins *et al.* 1989; Clare *et al.* 1987). As shown by Clare and Singh (1990), a change in environmental conditions will influence the life history parameters (e.g. life cycle duration, pupal weight, fecundity). Netted cages or perspex tubes are used for mating, with plastic or paper sheets adhered to the walls for oviposition. A food source (honey or sugar solution) should be provided. Washing in a 5% sodium hypochlorite solution (Clare *et al.* 1987) is usually used for cleaning the apparatus.

Rearing with an artificial diet provides many advantages, such as reduction in labour and colony maintenance. However, there are some limitations to rearing with such a method. These are common points of interest in the literature as methodical improvement is required. The effect of nutritional deficiency has been demonstrated by a number of studies. Many of these conclude that rearing with an artificial diet can cause significant variation in life history parameters. For example, research with *Cydia pomonella* found that a higher percentage of insects reared on natural diet successfully developed into adults. However, those developed on an artificial diet (Howell and IMC diet) resulted in the emergence of fewer adults (Hathaway *et al.* 1971). However, Howell (1970) found optimal life history parameters in those reared on both the natural and artificial diets, as both diets met the nutritional requirements of the insect. As seen by Altwegg (1971), the tortricid *Zeiraphera diniana* (Guenée) did not survive on artificial media unless it contained larch, pine or spruce needle powder, as some constituents of host needles were required as a feeding stimulant for first instar larvae (cited in Benz 1991).

According to Bathon *et al.* (1991), three viruses are common to tortricid rearing colonies if reared in unsterilised conditions. These include the nuclear polyhedrosis virus, the granulosis virus, and microsporidia, all of which are effectively controlled by cleaning of eggs, pupae and rearing equipment.

It has been demonstrated that a change in sensitivity towards normally rejected host plants may eventuate in those developed on an artificial diet. Schoonhoven (1967) observed such an event with the sphingid, *Manduca sexta* (L.), and believed the change was related to a decrease in the sensitivity of the contact chemoreceptors.

Other limitations believed to be related to rearing with an artificial diet include prolonged development time, disrupted mating behaviour, sperm inviability, decreased fertility, egg hatch and sperm motility and adult malformations (Ochieng'-Odero & P. Singh 1992; Boller 1972); changes in pheromone production (Gast 1968); and inbreeding (Roush 1986). These limitations are related to an incompatibility and various deficiencies within the diet and methodology. In order for rearing to be optimal, the diet and methodology requires modification, of which depends on the species to be reared (Singh 1977; Bathon *et al.* 1991).

2.4.3 Differences in tortricid life history with diet

It has been demonstrated by various authors that insects reared on different diets experience a change in life history parameters (e.g. Delisle & Hardy 1997; Delise & Bouchard 1995; Howell 1970). Larval diet had a significant effect on the life history parameters of *C. pomonella*. When developed on a natural diet of immature apples, the average pupal weights of male and female were 34.5 and 43.4 mg, respectively. Whereas, those reared on Navon artificial diet had average male and female pupal weights of 24.3 and 28.8 mg, respectively. Furthermore the average fecundity of those reared on the apple diet was 75.7 eggs, whereas those reared on the artificial diet had an average fecundity of 73.9 eggs (Hathaway *et al.* 1971).

2.5 General biology of tortricids

2.5.1 Life history

Various tortricid species inflict direct or indirect damage onto various commodities through larval feeding, deeming them unmarketable. Given the economic importance of this family, accounts of the life history of pest species are common as such information is essential for the development of long-term management programs.

2.5.1.1 General outline

The life cycle of a tortricid occurs in four stages (egg, larva, pupa and adult). The larva typically develops through between four and eight instars, depending on the species (Benz 1991). However, developmental polymorphism may occur in those exposed to variable conditions. Under high temperatures, many species have additional instars as seen with the tortricid *Cydia molesta* (Russell 1986) (cited in Benz 1991). Schmidt and Lauer (1977) found that *Choristoneura viridis* Freeman underwent six, seven or eight instars when reared on an artificial medium. Furthermore, both *Choristoneura occidentalis* Freeman and *Choristoneura fumiferana* commonly developed through six instars, however, five and seven instars were also observed (cited in Schmidt *et al.* 1977). Larval instars are distinguishable by characteristic head capsule widths. Dyar (1890) (cited in Schmidt *et al.* 1977) quoted 'widths of the head of a lepidopterous larvae in its successive stages follow a regular geometrical progression'. Larval instars are typically determined by either direct observation of the larval stage or the range of collected head capsule width data (Schmidt *et al.* 1977). The estimation of the duration of tortricid life stages have been derived using a physiological time scale based on degree-days (DD), providing a basis for short-term forecasting of events in the life cycle of an insect pest (Benz 1991).

Common to many tortricids, is the onset of a diapausal stage during the final instar larvae. Diapausal states are often triggered by unsuitable environmental conditions, such as extreme temperatures and unavailability of host plants (Rothschild & Vickers 1991). It is possible to continuously rear most tortricids under the appropriate conditions, as diapause is a facultative state. Evidence suggests that diapause is primarily initiated by daily photoperiod and temperature conditions (Brown 1991). Dickson (1949) found the diapause of *Cydia molesta* to be primarily onset by absolute duration of daily photoperiod and temperature (cited in Rothschild & Vickers 1991). Further suggestions indicate that nutrition has a role in the diapause of *C. molesta*, however, such comments are speculative (Roehrich 1961) (cited in Rothschild & Vickers 1991). Dickson (1949) (cited in Rothschild & Vickers 1991) also found that the middle instars of some species including *C. molesta*, is where the influence is greatest for the onset of diapause. It is also possible that photoperiod has an earlier effect, such as on the egg during embryogensis. The breakage of diapause is not comprehensively understood. However, Russell (1986) (cited in Benz 1991) stated that discontinuation is an undefined interaction between temperature and photoperiod.

Larvae tend to feed for a critical period before pupation can occur. For example, *Cydia pomonella* failed to pupate when feeding was prevented during the final instar, and at least 48 hours of feeding had to occur within the final instar to obtain a 100% rate of pupation (Jans 1982) (cited in Benz 1991). This phenomenon has been termed the latent feeding period and is governed by attaining a critical weight specific for each species, i.e. a threshold for final instar larvae to pupate. Lower temperatures resulted in higher pupal weights due to an increase in the latent feeding period of *Cnephasia jactatana* (Walker) (Ochieng'-Odero 1991). Furthermore, Ochieng'-Odero (1990) found that the pupal and adult weights of *C. jactatana* were related to the duration of the latent feed. Therefore, it has been concluded that the reproductive performance and quality of an insect is dependent on the weight gained from larval feeding. A hypothesis was proposed by Ratte (1985) to explain development changes that occur under different temperatures. The growth rate and critical rate of an insect species are modified to compensate for sub-optimal temperatures (the dual-temperature hypothesis).

Late instar larvae, pupae and adults of the family Tortricidae demonstrate external sexual dimorphism. Dark elliptical bodies, i.e. testes, can be readily detected in the final instar larvae. Pupal size, weight, and the number of freely articulated abdominal segments differ between male and female, where the female has three visible segments, and the male has four. The adult female is generally larger in size and more robust than the male, with further differences evident in the external genitalia (Howell 1991).

The body size of an insect has conventionally been used as a primary indicator of its ecological and physiological properties. As seen in the literature, several theoretical and empirical studies have investigated the connection between body size and other life history traits, such as development time and reproduction (e.g. Resis 1989; Roff 1992; Klingenberg & Spence 1997). Other assumptions, such as the connection between age and fecundity (Sterns 1992), exist in the theory of life history. A positive correlation between such traits is not always the case (e.g. Klingenberg & Spence 1997), indicating the lack of trait adaptation in these instances. The issue of body size is further explored in section 2.4.3.3.

2.5.1.2 Tortricids in New Zealand

In New Zealand, representatives of the tortricid family (native and introduced) are more commonly found within the sub-family Tortricinae (Dugdale 1966). The species present have adapted to a wide range of fruit and vegetable crops and ornamentals. Many of these tortricids share common attributes, including polyphagous feeding behaviour, a multivoltine nature, and are morphologically variable within the species. A nationwide tortricid survey was conducted between 1974 and 1977 (Chapman & Lienk 1971), identifying the following as primary economic species: in horticulture, *Ctenopseustis obliquana*, *Planotortrix excessana* (Walker), *Epiphyas postvittana*; and in silviculture, *P. notophaea* (Turner). Between two and four generations exist per year for these species (Wearing *et al.* 1991). Many other tortricid species in New Zealand have less economic impact.

A common representative from the sub-family Olethreutinae in New Zealand is *Cydia molesta*, a pest of pome and stone fruit crops (Wearing *et al.* 1991). The eggs of *C. molesta* are a flattened oval shape and are typically laid singly. Under constant laboratory conditions, this tortricid develops through four or five larval instars (Rothschild & Vickers 1991). The complete life cycle of *C. molesta* ranges from 30 to 49 days; with the egg stage taking 4-8 days; the larval stage lasting 12-22 days; the pre-pupal stage taking 3-12 days; the pupal stage lasting 10-16 days; and with an adult longevity of 12-15 days (Rothschild & Vickers 1991). The average potential fecundity of *C. molesta* is 140 eggs per female (Rothschild *et al.* 1984).

2.5.1.3 Influence of abiotic and biotic factors on the life history of tortricids

2.5.1.3.1 Adult diet

The influence of adult diet on the quality and performance of a herbivorous insect has been examined. Howell (1981) found that the provision of an adult food source significantly increased the longevity of *Cydia pomonella*. Mating, oviposition and egg viability were not affected by the adult food provision. Conflicting results reported that oogenesis was only possible when at least water was supplied (Weismann 1935; Geoffrion 1959) (cited in Howell 1981). It has been concluded that prolonged longevity is not necessarily desirable, as many tortricids oviposit the fertile egg load within the first week, and any deposited after that are often infertile. Of eggs laid by *C. pomonella*, 90% were oviposited within the first two to five days (Howell 1981).

2.5.1.3.2 Environmental conditions

Howell (1981) demonstrated that humidity and temperature outside the optimal range, decreased the fertility of eggs laid, and they negatively affected the mating, oviposition, and longevity of *Cydia pomonella*. However, increased temperatures up to 26.7°C have been known to enhance mating (Howell 1981), and colder temperatures down to 20 °C resulted in a further increase in adult weight, fecundity and longevity of *E. postvittana* (Danthanarayana 1975), irrespective of larval host plant. Such variation is attributable to the variety and quality of the food plant material available, i.e. the presence of more nutritive leaves throughout the cooler months of the year.

2.5.1.3.3 Larval host plant

The nutritional requirements of Lepidoptera include various proteins, carbohydrates and lipids for most species. Proteins are important components of the larval diet, and the value of the food plant depends on the contents and availability of essential amino acids (Benz 1991). As adults are unable to assimilate protein, the requirements for egg development must be derived from reserves laid down by larvae (Wigglesworth 1972). Carbohydrate requirements differ between most species and throughout larval development. Certain carbohydrates such as sucrose and inositol may be necessary for the stimulation of feeding (Schoonhoven 1969). Little is known about the physiology of phagostimulants and deterrents in Tortricidae.

In accordance with Danthanarayana (1975), variation in temperature and larval host plant has an effect on the developmental rate, size and fecundity of various tortricid species. Larval diet plays an influential role in determining the fecundity of *Epiphyas postvittana*, due to the physiological and chemical differences between food plants. Various studies have shown that larval diet also affects the body size of the tortricids *E. postvittana* (Dumbleton 1939; Thomas 1965 cited in Tomkins *et al.* 1989; Danthanarayana 1975) and *Ctenopseustis obliquana* (Green 1975 cited in Tomkins *et al.* 1989). *Archips argyrospila* Walker and *Archips rosana* were reared on ten different host plants, of which development rates differed on all species (Smirle 1993). Difference in pupal weights were also evidence, but was not correlated to fecundity. Unsuitability was possibly due to the presence of cyanogenic glycosides in the tissues of some plant species. Barrington *et al.* (1993) examined the development parameters of various New Zealand tortricids fed with six native plants. Two of the plant species inhibited development, whereas four reduced fecundity and egg survival in

one of the tortricids. Furthermore, the tortricid *Planotortrix excessana* had a low larval survival and adult emergence, with pupation deformities whilst feeding on one of the plant species tested. This was believed to be related to the presence of active limonoids isolated from the plant (Barrington *et al.* 1993).

2.5.2 Host plant associations

Herbivory is believed to have evolved independently throughout several insect orders, making plant feeding a widespread phenomenon. Evidence in some insect species implies that co-evolution occurred between phytophagous insects and their host plants (Prokopy & Owens 1983; Ehrlich & Raven 1964). However in reality, clear examples of such appear to be rare. Jermy's theory of sequential evolution appears to be the most applicable to the greatest range of insect families (Jermy 1976). The theory implies that plants evolved a complex of chemicals and adaptations in response to a variety of abiotic factors, consequently insects evolved to adapt to these (Chapman & Kennedy 1976).

2.5.2.1 Host plant selection of herbivorous insects

The host finding and selection by an insect integrate a complex of morphological, physiological and environmental stimuli, which attract or deter various species, depending on their historical associations and other abiotic or biotic factors. Generally, host selection is recognised as incorporating a series of steps. Various authors (e.g. Bernays & Chapman 1994) have reviewed the steps and found that such behaviour includes host habitat finding, host finding, recognition, acceptance and suitability.

Varying proportions of visual, mechanical, gustatory, and olfactory stimuli mediate the host selection process for an insect. For optimal discrimination, each insect species has evolved unique sensory apparatus designed to distinguish hosts from non-hosts. Apparatus for detecting stimuli from the external environment include compound eyes, ocelli, mechano and chemoreceptors, and for detecting the internal environment include detectors of various physiological and reproductive states (Stadler 1977). Sensory cues interact during selection, in which the appropriate behavioural response is instigated (Courtney & Kibota 1990; Dethier 1982). As pointed out by Chapman and Kennedy (1976) and Visser (1986), host selection is not based on mutually exclusive stimuli but on an array of stimuli acting synergistically to trigger the corresponding behavioural response.

Singer (1982), Wiklund (1981), Thompson (1988), and Courtney (1986) believe that a range of hosts exist for most insects. Courtney *et al.* (1989) proposed a general model for individual host selection, known as the hierarchy threshold model of host choice. The model states that host selection for oviposition will depend on the acceptability of each host assessed, with each choice governed by innate tendencies and past experience. These will inevitably result in a ranking of all the plants assessed. Therefore, Rausher (1978) concluded that overall host plant use of an insect population reflects individual differences in behaviour.

2.5.2.2 Stimuli mediating host selection

In accordance with Thompson and Pellmyr (1991), allelochemicals, nutritional chemistry, plant morphology, feeding modes, and the interaction of these factors have been recognised as major determinants of host preference and specificity. Given their predominant role in host selection, these factors are considered in more detail.

2.5.2.2.1 Chemical cues

A balance of sensory information from a potential host combined with the internal state of an insect ultimately determines whether the plant is to be accepted or rejected for oviposition (Miller & Strickler 1984). The chemical constitution of a plant plays a significant role in determining this association, as most insects use olfaction and contact chemoreception as primary mediators for resource location (Thorsteinson 1960).

Leaf surface chemicals have been comprehensively reviewed by Städler (1986), and the compelling influence of such stimuli on the behaviour of insects, particularly lepidopterans, was demonstrated. Volatile compounds are released from the plant stomata, as a result of the oxidative degradation of leaf lipids. Volatiles are typically carried down-wind in a series of air pockets, and this allows an insect some distance away to perceive the odours associated with that plant. The concentration of the odour depends upon a number of factors including the amount of volatile released, the number of other compounds within the airflow, the distance between the plant and insect, the nature of the terrain, and the wind conditions (Bernays & Chapman 1994). Volatiles include a variety of compounds such as water, alcohol, aldehydes, ketones, esters, aromatic phenols and lactones (Bernays & Chapman 1994).

According to Hodkinson and Hughes (1982), the leaves and reproductive parts of the plant generally provide the greatest nutritional value for many insect species. Compounds representative of the nutritional state of the plant (Dethier 1976) are perceived by the insect's chemoreceptors on contact with the plant, and may generally have a stimulating effect (especially the sugars, which tend to be phagostimulants), if compatible with the insect's requirements. Furthermore the concentration of particular chemical compounds, or the relative proportion of compounds present, will determine the preference the insect shows for the plant.

Additional compounds present within some plant species are the secondary metabolites or plant allelochemicals, e.g. n-aliphatic alcohols and aldehydes, isoprenoids, various glycosides, and phenyl propanes, which play a significant role in the host selection of insect herbivores, by acting as attractants or deterrents (Kogan 1977). A number of functions have been ascribed to these compounds such as protecting the plant from insects and pathogens by deterring certain species (Dethier 1976). It is known that many secondary plant metabolites cause certain insect species to avoid feeding on such plants. However, there is much dispute against the idea that such allelochemicals evolved solely as a defence mechanism against insects (Jermy 1976), and the precise role of secondary plant compounds remains unknown.

A chemical stimulus is perceived by sensilla, present on the insect's antennae, mouthparts, legs and ovipositor (Hanson 1983; Dethier 1976). As indicated by Deither (1976), sensory apparatus on the insects' body enables volatile detection, whereby odour-conditioned anemotaxis directs the insect toward the source. Host finding aided by olfaction is known to consist of two main mechanisms: arousal and orientation (Bernays & Chapman 1994). The initial arousal of a host-searching insect is typically followed by a dispersal action, in which the insect orients itself towards the source of the stimulus. Once orientated to the stimulus source, an insect may continue to approach the plant and possibly land on it. Many studies indicate that chemical stimuli play a key role in host recognition and acceptance, after contact has been made with the plant (Feeny *et al.* 1983; Foster & Harris 1992a). Waxes and other plant surface compounds may contain species-specific compounds, which influence acceptance. According to Bernays and Chapman (1994), wax chemistry is known to affect the host selection of aphids, planthoppers, and grasshoppers. Receptors enabling contact chemoreception, occur throughout most parts of an insect's body including the

wings, antennae, ovipositor, tarsi, palpi and proboscis (Städler 1977). The Hessian fly, *Mayetiola destructor* (Say), repeatedly antennates foliar surfaces and drags its ovipositor over the surface, thus bringing both chemical and mechanical receptors in closer contact with cues at the plant surface (Harris & Rose 1989; Harris & Rose 1990).

Harris and Rose (1990) found that the removal of chemical cues caused significantly larger reduction in egg lay for *Mayetiola destructor*, than with the removal of either tactile or colour stimuli. The primary cue for host selection for the tortricid *Choristoneura fumiferana* has been reported as host shape and chemical composition (Greenbank 1963) (cited in Stadler 1974), but conflicting results have since been found indicating that chemical stimuli are the primary cue for host selection of this species (Schoonhoven 1968, Fraenkel 1969; Städler 1974). Fox and Morrow (1981) highlighted numerous examples in which both visual and chemical stimuli operate sequentially or simultaneously in the host plant location of various herbivorous species. Furthermore, Aluja and Prokopy (1993) stated that it is increasingly apparent that most insects respond to an array of host stimuli. For example, the host location of the dipteran *Delia antiqua* (Meigen) and *Rhagoletis pomonella* (Walsh) is contingent upon the appropriate combination of structural, visual and chemical characteristics, of which all have a synergistic effect (Harris & Miller 1983).

2.5.2.2.2 Visual and tactile cues

Any response to plant chemistry is typically combined with visual and/or tactile stimuli to achieve a finer degree of precision. Subsequent attraction results from a positive response to the morphology of the host plant, i.e. leaf colour, size, shape, orientation, surface texture, etc (Bernays & Chapman 1994). Visual orientation is an integral part of host selection for most herbivorous insects, proven to be of particular importance for aphids, whitefly, thrips and butterflies (Kogan 1977; Feeny *et al.* 1983). Three primary properties serve as visual cues for insects, including spectral quality, dimension and pattern of the potential host and its environment (Prokopy & Owens 1983). Bernays & Chapman (1994) concluded that the colour and pattern of a host plant are important in the final stages of host selection, particularly in day flying insects. Additionally, any variation in wavelength and light intensity may give rise to species-specific responses (Prokopy & Owens 1983). For example, pollinating insects have more efficient foraging behaviour when the colours are associated with food. The honey bee, *Apis mellifera* (L.), learns most quickly when the colour was violet (410 nm)

and learnt more slowly when the colour was blue-green (490 nm) (Barth 1991). Typically, many herbivorous insects show attraction towards yellowish hues (520-600 nm), enabling discrimination between foliage and non-foliage like hues (Harris & Miller 1983). Orientation to a potential host is further aided by horizon characteristics and contrasting backgrounds. Using the shape and size of a host plant as cues contrasting with the background may aid host finding and recognition, especially towards an individual host at close range (Prokopy & Owens 1983).

Other physical properties of the leaf surface that may influence host selection include the presence of hair or trichomes. Such epidermal appendages can present formidable obstacles to some insect species, however, in some insect species they are not regarded as an impediment. Tomkins *et al.* (1991a) found that many leafroller species lay eggs close together in batches, and they speculated that this was to avoid the obstruction of trichomes. Such a function would not be relevant to moths that lay eggs singly, e.g. *Cydia pomonella* (Hagley *et al.* 1980). In general, tactile stimuli are known to play an important role in the host choice for a variety of herbivorous insect species. Mechanoreceptors are usually located on the insect's ovipositor, antennae and tarsi, enabling access to cues about leaf geometry and consistency of the leaf substrate (Henrich 1971). Degan and Städler (1997) stipulate that physical attributes are strong stimuli during the final steps of host selection for phytophagous flies.

2.5.2.3 Non-plant factors influencing behaviour

The host selection behaviour of an insect can be influenced by a number of internal and external environmental factors. As concluded by Edwards and Wratten (1980), external factors such as temperature, humidity, rainfall, wind intensity, solar radiation, nutrient levels, seasonal factors, and temporal factors, may increase or decrease the suitability of a host plant. Furthermore, various authors have demonstrated that plant density and availability, herbivore density, and the presence of other plant species, could also affect the suitability of a host plant (Stanton 1983; Papaj & Rausher 1983; Hodkinson & Hughes 1982).

In order for feeding, growth and reproduction of a herbivorous insect to be successful, internal factors such as learning ability, experience, physiological state, age, mating status, host plant deprivation, and various other factors must be optimised (Bernays & Chapman 1984). The learning capabilities and experience of an insect will

alter host plant associations, and the effectiveness of host plant selection in a variable environment. Various phenomena, resulting from adult experience, have been demonstrated. These include chemosensory adaptation, sensitisation, nutrient-related sensillum changes, sensillum changes from plant secondary compounds, habituation, aversion learning to toxins and nutrients, associative learning, and inductions to foods (Bernays & Chapman 1994). Discovering which of these phenomena are acting upon an insect to influence its host selection behaviour, is however, a complicated process.

Limited evidence has demonstrated that host plant selection can be influenced by genetic differences within and between insect populations. Variation of this type has been attributed to different species biotypes, which may differ in their ability to select certain host species. Behavioural diversity may also manifest between insect populations, especially if gene flow is limited. Little is known about the mediation of such variation (Bernays & Chapman 1994). However, it is believed related to small differences in the sensitivity of receptor systems and the central nervous systems.

2.5.2.4 Host selection bioassaying

The host selection bioassay has been used extensively to examine the host plant preference of an ovipositing insect in a controlled environment for purposes of testing resistant cultivars or potential biological control agents. Assays of this nature are commonly performed in a multiple-choice arena where a group of sexually mature females are introduced. However, Thompson and Pellmyr (1991) stated that such host selection bioassays are commonly flawed in their design, as variation in preference is a composite of individual variation. It was also stated that such confinement results in competition for oviposition sites, possibly leading to a more uniform distribution in oviposition, thus highlighting the need for individual testing of ovipositing females. Assays of this type have also resulted in random and arbitrary oviposition (Stange 1997; Day *et al.* 1997). Withers and Barton Browne (1998) explained that some occurrences may be a result of the inhibitory cage environment, central excitation and sensitisation of the ovipositing female, absorption of volatile kairomones, and/or reduced life expectancy. This review also suggested several modifications to the host selection bioassay for prevention of such symptoms. Some researchers prefer the use of no-choice or sequential choice tests for examining preference and acceptance, as the indices of host use are more relative (Courtney *et al.* 1989). However, if multiple-choice assays were optimally designed for the species in question, quality of results

would not be comprised. Additionally, Wearing (1998) concluded that at least ten replications are required in a bioassay to address any variation in egg laying. He also concluded that a more precise time frame and the use of only mated female moths could further reduce variation. Host selection is a multifaceted behaviour, from which each selection governs the host plant associations of the insect in the future. The evolution of new associations and the maintenance of current ones are dependent on the biology, reproductive success, and the phenology of the insect

2.5.3 Reproductive behaviour

Reproductive behaviour usually occurs as a series of patterns characteristic to each species. Within the tortricid family, it has been recognised that such patterns can occur as fairly simple routines, as with *Choristoneura fumiferana*, or consist of more complex patterns, such as the reproductive behaviour of *Cydia molesta* (Baker & Cardé 1979) and *Cydia pomonella* (Castrovillo & Carde 1980). The reproductive process is based around a plethora of stimuli utilised for the identification of a suitable mate for reproduction. This includes the detection of female sex pheromones and/or male sex pheromones, tactile stimulation, and visual stimulation through display, wing colouration, size etc. Reproductive behaviour is subject to intrinsic and extrinsic factors, therefore, any perturbation in optimal conditions usually results in behavioural changes that may reduce the reproductive output or success of an insect.

2.5.3.1 Reproductive behaviour of tortricids

Studies within the family Tortricidae indicate that reproductive behaviour is initiated by a calling female, which extends her abdominal tip to expose the pheromone gland thus releasing the pheromone (Benz 1991). The male usually responds to a female-emitted pheromone with a combination of antennal elevation, activation and flight, upwind orientation, courtship display and copulatory movements (Bartell & Shorey 1969). Variations to this process occur between tortricid species. Sanders and Lucuik (1992) examined the reproductive behaviour of *C. fumiferana*, in which the behavioural sequence of the male leading to copulation included searching, contact, spreading of claspers, and copulation attempts. The review made by Howell (1991) provides a comprehensive overview to the reproductive activity of *C. pomonella*. The female releases a pheromone, which the male orients towards through a series of zigzag movements, whilst rapidly wing-fanning. On approach, visual cues are utilised for finer precision. The male aligns himself along the female, clasping the abdomen and moving

into position 180° behind the female for commencement of copulation (Benz 1991; Castrovillo & Cardé 1980). Ferro and Akre (1975) found that virgin males were usually in copula for 40-60 minutes, but previously mated males copulated for longer, approximately 70-80 minutes (cited in Benz 1991). Baker and Cardé (1979) described the more complex reproductive pattern of the tortricid *Grapholitha molesta* (=*Cydia molesta*). This is typically pursued as a series of multiple rhythmic extrusions and retractions of male hairpencil organs, claspers and wings, and incorporates various chemical and anemo-tactile (wind movement) stimuli. The rate of reproductive success in this species is related to the accuracy at which courtship is performed (Baker & Cardé 1979).

The rhythm of reproductive activity has been extensively studied in the tortricid species *Epiphyas postvittana*. Most individuals from this species have been observed calling on the first day after emergence (Lawerence & Bartell 1972). Female *E. postvittana* performed a mating flight or fledging throughout the first four days, and the male during first five days (Gu & Danthanarayana 1990). A peak in oviposition occurred between days three and five for *E. postvittana* (Riedl & Loher 1980; Batiste *et al.* 1973). In the tortricid *Zeiraphera canadensis* Mutuura and Freeman, oviposition was initiated at sunset and was evident for up to three hours thereafter, with most mating occurring between 22.00 and 04.00 h (Quiring 1994). This pattern was similar to *Cnephasia pumicana* Zellar where mating was observed in the final three to four hours of the insect's active period i.e. the scotophase, and oviposition was concentrated between dusk and the fifth hour of this phase (Chambon 1976).

2.5.3.2 Internal control of reproduction behaviour

In accordance with Mbata and Ramasway (1990), the rhythm of reproduction and pheromone production in most lepidopterous species is controlled by a neuro-secretion, the neuro-hormone (PBAN) derived from the sub-esophageal ganglion complex within the brain. A clear relationship has been demonstrated between the effect of intrinsic and extrinsic factors on pheromone production in various lepidopteran species (e.g. Webster & Cardé 1982; Mbata & Ramasway 1990).

Copulation usually results in a decrease of the pheromone content and/or sexual receptivity of an insect (Gillot & Friedel 1977; Webster & Cardè 1982; Mbata & Ramasway 1990), suggesting the possibility of receptivity inhibiting factors

being initiated after copulation. This is believed to occur in a number of ways. Firstly, the physical presence of sperm, or spermatophore in female reproductive system may stimulate stretch receptors, exerting a pheromonostatic effect on pheromone glands, sending signals that inhibit pheromone production (Thornhill & Alcock 1983). This is common in cockroaches (Roth 1962) and *Pieris* butterflies (Sugawara 1979). Secondly, males of various lepidopteran species are equipped with external mating plugs (sphragis), which function to obstruct the genital claspers of subsequent partners (Thornhill & Alcock 1983). Finally, the male may deposit a pheromone inhibitory substance limiting production and/or receptivity, or trigger pheromonostatic response. In many lepidopteran species, total pheromone concentration remains high immediately after mating, dropping thereafter and remaining low. However, the concentration may peak again in those that mate more than once (Thornhill & Alcock 1983).

2.5.3.3 Influence of biotic and abiotic factors on reproductive success

Studies have found that reproductive behaviour is predominately influenced by biotic factors such as age, body size and the degree of multiple mating (polyandrous species only), and furthermore, by abiotic factors, including temperature, photoperiod and larval host plant (Baker & Cardé 1979). Such factors usually have a large impact on the rhythm and overall reproductive success of an insect.

Various authors have explored the hypothesis that age can affect the reproductive success of tortricids. Foster *et al.* (1995) found that various tortricid species demonstrated a change in copulation time, sex pheromone titre, number of eggs laid in relation to first mating, frequency of copulation, flight response and responsiveness of the male to the sex pheromone, with increasing age. Furthermore, Delisle (1995) demonstrated that the reproductive success of female *Choristoneura rosaceana* (Harris) reduced with age. Karalius and Büda (1995) found that the reproductive success was maximal when *Ephestia kuehniella* (Z.), *C. pomonella* and *Yponomeuta cognagellus* Hbn. were mated on the first, third, and third to seventh days after emergence, respectively. The occurrence of later mating resulted in an increase in the infertility of *C. pomonella* and an increased longevity of all three species examined.

Polyandrous insects generally acquire enhanced reproductive success from multiple mating (Ridley 1988) (cited in Danthanarayana & Gu 1991). Numerous hypotheses have been generated to explain the evolution of multiple mating, including

the increase in genetic heterogeneity of offspring; somatic maintenance; enhancement of female survival and fecundity; and the replenishment of inadequate sperm supply to compensate for inadequate mating (Walker 1980; Drummond 1984; Loman *et al.* 1988). Multiple mating is known to occur in several tortricid species including *E. postvittana* (Danthanarayana & Gu 1991; Foster & Ayers 1995), *Choristoneura fumiferana* (Outram 1971), *Cydia molesta* (George & Howard 1968) and *Cydia pomonella* (Howell *et al.* 1978). For example, *E. postvittana* mates an average of 3.5 times throughout a life span (Geier *et al.* 1978), and this has been found to improve its reproductive success as a result of increased fecundity and fertility.

Female weight is generally recognised as an index of potential fecundity (Geier 1963), which can in turn be related to the reproductive success of an insect. Such an index is based on the premise that a correlation exists between the numbers of oocytes in the ovarioles and the weight of the female, but doubts about the generality of this hypothesis do exist (e.g. Leather 1988). Cisneros *et al.* (1974) found that *C. pomonella* confirmed the hypothesis. Geier (1963) demonstrated that female *C. pomonella* weighing 20 mg produced around 100 eggs, however, females heavier than 40 mg produced approximately 208 eggs. In accordance with Tammaru *et al.* (1996) it has been shown that body size was the main determinant of female reproductive output for the geometrid *Epirrita autumnata* Borkhausen. This association is common among many other insect species and contributes in explaining why males of various species prefer larger females. Reports on several insect species have found a further correlation between male body size, life span and female choice (Neems *et al.* 1990; Banks & Thompson 1985). However, contradictions to such findings also exist (e.g. Tammaru *et al.* 1996).

In most lepidopteran species the timing and occurrence of reproductive activities, such as female pheromone release and male responsiveness, are modified by external cues such as photoperiod and temperature. For example, *Cydia pomonella* is entrained by daily photoperiod, and activity also varies with season, location and temperature. The adults are typically active between the hours of sunset and two hours after, with a steady decline of sexual activity evident thereafter. Change in temperature also influences the reproductive success of an insect. This was demonstrated by Delisle (1995) and Howell (1981), in which a significantly lower proportion of successful

mating occurred outside the optimal temperature ranges of *Choristoneura rosaceana* and *Cydia pomonella*.

The larval nutrition of a male tortricid contributes to the reproductive success of an insect population. Delisle and Bouchard (1995) concluded that a positive relationship exists between male quality, larval diet, age and the reproductive success of *Choristoneura rosaceana*. There was a significant increase of re-mating in males when larvae were developed on a higher quality food. Furthermore, the theory states that females that consume less suitable larval host plants will be less fecund, resulting from a reduction in size and reduced nutrition for the development of eggs (cited from Delisle & Bouchard 1995). The reproductive behaviour of an insect, in particular a tortricid, is a complex process incorporating and integrating various biological, physiological and ecological facets. In order for success to be maximised, optimal intrinsic and extrinsic conditions must occur.

2.6 Phenology of tortricids

The ecology of tortricids in their natural environment has been examined for a range of pest species. Tortricid pests are more common to the temperate regions as environmental and habitat conditions are more suitable. However, those that exist in less suitable environments develop though an overwintering stage, which may initiate developmental diapause. Chapman (1973) examined forty-one tortricid species existing on apple from different regions, of which many were univoltine, and others that developed through two to five generation per year. *Cydia molesta* was observed to develop through up to seven generations per year. Research into the phenology of tortricids has been undertaken for many years, typically forming the basis for development and implementation of insect pest management strategies. Various methods of research have evolved which are still advocated for current day study. These include sustained sampling on one or a variety of sites, visual assessment of eggs and larva over time, and the use of synthetic sex pheromone for trapping, all of which typically result in the generation of life tables and simulation modelling.

2.6.1 Factors influencing the phenology and abundance of tortricids

Tortricids existing within cooler regions typically develop through one generation (univoltine) per year and occasionally take up to two years to complete a full life-cycle. Whereas, those in warmer climates occur through several generations per year

(multivoltine). Solomon (1991) stated that the number of generations that a tortricid undertakes is primarily determined by climatic factors. Geier (1963) found that favourable permitted *C. pomonella*, to have a trivoltine life cycle within the Capital Territory of Australia. The main regulatory factors in this location were identified as food supply, competition and limited supply of larval shelters for overwintering individuals. Evidence from other regions such as Canada, Nova Scotia and New Zealand have also identified similar factors regulating the populations of *C. pomonella*, as well as the warmth and duration of the spring and summer seasons (Audemard 1991; Putman 1963; Wearing 1979). It was also found that a significant relationship existed between the number of generations per year and latitude, with more generations occurring in temperate regions (Bovey 1966; Riedl & Croft 1978) (cited in Solomon 1991). *Epiphyas postvittana* developed through between two and four generations per year in New Zealand (Wearing *et al.* 1991), with day length and climatic conditions indicated as the primary regulatory factors.

Natural enemies are important population regulators for most species of tortricids. In has been demonstrated by Varley *et al.* (1973) that natural enemies have a strong influence, particularly on forest insect populations. Evidence indicates that parasitoids and predators negatively influence the abundance of *Choristoneura fumiferana*, with other factors such as forest maturity, weather variations, food supply, dispersal flights of the moths and forest management, also contributing to variations in abundance (Varley *et al.* 1973). The population ecology of *Epiphyas postvittana* was shown to be influenced in part, by predation and parasitism in Australia (Danthanarayana 1983).

2.6.2 Natural enemies of tortricids

Tortricids are attacked by a variety of natural enemies that ultimately play a critical role in the regulation of many species (e.g. Thompson 1943-1964; Herting 1975; van der Geest & Evenhuis 1991). Predators of tortricids include insectivorous birds, small mammals and a variety of arthropod species, which feed on all life stages of the tortricid. Mills and Carl (1991) indicated that spiders are of particular importance in arboreal environments, whereas, ant species have been found to be of primary importance in the dynamics of a forest environment. Danthanarayana (1983) found that spiders significantly contributed to the mortality of older larval instars of *E. postvittana*. Campbell and Torgersen (1982) found that *Camponotus* species preyed on *Choristoneura occidentalis*, significantly reducing population numbers. Overall,

predation is an effective regulator of a tortricid population particularly when the pest is at low densities and when predators target life stages with the longest duration (Hassell 1985).

Egg parasitoids of the Tortricidae family are typically restricted to the genus *Trichogrammatidae* in New Zealand. Braconid egg-larval parasitoids have been identified from the genera *Ascogaster* and *Phanerotoma* (Mills & Carl 1991). Furthermore, larval parasitoids have been identified within a variety of insect families including Braconidae, Ichnuemonidae, Chalcidoidae, Bethylidae, Tachinidae and Sarcophagidae (Mills & Carl 1991), many of which are present in New Zealand. *Epiphyas postvittana* is attacked by a complex of larval parasitoids including species from the genera *Goniozus*, *Apanteles*, *Cotesia*, *Ophion*, and species *Pales funesta* (Hutton), *Pales feredayi* (Hutton) and *Trigonospila brevifacies* within New Zealand orchards (Wearing *et al.* 1991). According to Green (1984) parasitism of *E. postvittana* varies from 19.4 to 30.2% in the Auckland region. The role of these natural enemies on the regulation of populations is still not understood. Pupal parasitoids of tortricids have been identified from many insect families including Ichnuemonidae and Chalcidoidae (Mills & Carl 1991). The role of parasitoids has been studied widely in various forest habitats, and examples cited within Mills and Carl (1991) indicate that egg parasitism varied from 0 - 30%; larval parasitism varied from 1- 60% and pupal parasitism from 5 - 70%, this included examples from New Zealand.

The predominant groups of pathogens infecting tortricids include viruses, bacteria, fungi and protozoa (Zimmermann & Weiser 1991). Even though tortricid larvae are typically contained within a relatively protected niche, wind, rain or encounters with other insects may result in the introduction of such organisms.

2.7 Insect pheromones

2.7.1 The nature of olfactory communication

Millions of years of evolution have resulted in specialized visual, tactile, acoustic, and olfactory modes of insect communication. Used extensively by insects, the olfactory channel provides an effective method of biological communication, in which insects utilise specific chemicals, to act as molecular messengers between individuals (Agosta 1992). The use of chemicals for communication has been conclusively

demonstrated in many organisms including higher animals, insects, algae, fungi and bacteria (Birch 1974). Wilson (1970) has reviewed chemically mediated behaviour in the principal invertebrate phyla, as well as fungi and algae.

French naturalist, Jean Henri Fabre, first recognized olfactory communication between insects over 100 years ago. Through simple experimentation, he discovered the attraction of the male oak eggar moth (*Lasiocampa quercus* L.) and the male great peacock moth (*Saturnia pyri* (L.)) to caged virgin female moths, respectively (Howse *et al.* 1998). The males of both species were attracted to an empty cage after the females had been removed. From such observations it was concluded that specific chemicals were involved in communicating between individuals.

It was not until recently that the knowledge of olfactory communication flourished, resulting in the development of specific terminology and categorization. Chemicals involved in communication between organisms were coined as semiochemicals (Law & Regnier 1971). Subsequently, it was recognised that some chemicals were used to communicate intraspecifically whilst others were used for interspecific communication. Therefore, in 1971 Whittaker and Feeny sub-divided semiochemicals to include pheromones (intraspecific communicators) and allelochemicals (interspecific communicators). Additionally, Brown *et al.* (1970) proposed the terms kairomone and allomone to include allelochemicals that benefit the receiver and the sender within an interspecific action, respectively. Research on semiochemicals has since flourished, with research typically concentrating on insect pheromones and their practical application.

2.7.2 The nature of insect pheromones

During the 1970's, it was widely accepted that pheromones served as intraspecific communicators and that pheromonal communication was also possible on an interspecific level, e.g. predators and parasites (Whittaker & Feeny 1971). Since the progression of pheromonal science, certain characteristics have been recognized as the backbone for understanding chemical communication. The general characteristics of pheromones were reviewed by Birch (1974).

- Pheromones are generally active in minute quantities and usually induce a response with a single molecule, compound or mixture.
- Pheromones are highly specific, in that they evoke intraspecific behaviour.
- Pheromones are generally multi-component hence multi-functional systems.
- Individual components of a pheromone are inactive alone and must synergise with other components to evoke a response.
- The information carried by molecular messengers is optimised through gland morphology, wind current, pheromone concentration and compound nature.
- Pheromones mediate the behavioural and physiological activities of an insect, activities ranging from mate location to caste determination of social insects.

Insects produce a wide range of pheromones, many have been reviewed by various authors (Jacobson 1972; Howse *et al.* 1998). Pheromones can be categorized either by the kind of activity they mediate (Shorey 1973), or their biological function (Birch 1974). For example, sex pheromones are produced by the male and/or female, stimulating behavioural reactions in the opposite sex, which directly or indirectly results in mating behaviour (Howse *et al.* 1998). Other insect pheromones exist for purposes including aggregation, alarm, defence, social, dispersal, recruitment, oviposition, territorial and developmental functions (Galbreath 1982; Shorey 1973).

2.7.3 Insect sex pheromones

Sex pheromones are the most diverse and explored of the insect pheromones, and consequently have been identified for large number of insect pests, particularly lepidopteran species (Pherolost 2000; Arn *et al.* 1992; Booij & Voerman 1984). The first insect sex pheromone identified was by a German chemist, Adolph Butenandt, in 1959 (Schneider 1992). The active component, widely known as Bombykol, was isolated from 250 000 abdominal tips of the female silk moth, *Bombyx mori*.

Female sex pheromones have been extensively researched, of which examples can be found in section 2.7.4. Male sex pheromones of various species have also been examined of which stimulate the female to fly upwind, and aphrodisiacs which exert a direct effect on the females' nervous system increasing the likelihood of copulation. Other stimuli such as structural features, e.g. hair-pencils, visual and auditory stimuli are commonly associated with sexual behaviour (Jacobson 1972). Two classic examples of male sex pheromones are the moth *Hepialus humuli* L. that releases an

odour from a brush located on the hind leg which the female detects with antennal receptors. The male butterfly *Danaus plexippus* L. has brush like structures (hair-pencils) that serve for pheromone dissemination; release being an important pre-requisite for female attraction and acceptance (Jacobson 1972).

Techniques enabling identification of pheromones have become more powerful and a lot simpler in the recent decades. The identification process incorporates a variety of chemical and behavioural bioassays. The methods for extraction currently employed include gland excising (Foster & Roelofs 1987); solvent extraction, immersion, or washing of the pheromone gland (Webster & Cardé 1982); trapping the pheromone volatiles in an absorbent material such as Porapak Q, Tenax, charcoal, glass wool or beads, using an air current or inert gas (Bjostad *et al.* 1980). The above techniques are generally preceded by combined gas chromatographic and electroantennogram analysis or other detection techniques (Howse *et al.* 1998; Arn 1991; Foster *et al.* 1990; Struble & Arn 1984).

2.7.3.1 Production of pheromones

Lepidopteran pheromones are typically produced through a series of chain-shortening and desaturase steps (Roelofs & Wolf 1988). The pheromone components reside within the exocrine glands, defined as modified epidermal cells originating from the insects' integument (Percy & Weatherston 1974). The glandular cells are either cuboidal, columnar, modified columnar, or goblet in shape and consist of a large nucleus, and many vacuoles. The pheromone is produced within the glandular cells, transported and disseminated through the cuticle. Richards (1927), Jacobson (1972), and Percy and Weatherston (1974), all give detailed accounts on glands associated with the pheromone production of several insect orders. Female tortricid pheromone glands exist as dorsal invaginations between the eighth and ninth abdominal segments. The glands are comprised of eversible folds to increase surface area, or sacs of glandular tissue. According to Percy and MacDonald (1987), the glands of eleven Olethreutinae species have been examined and the intersegmental membrane is invaginated and forms a dorsal sac. Pheromone scent scales are common in male tortricids, with a presumed function of keeping the females stationary prior to copulation (Grant 1978). Male pheromone scales can be located the forewing coastal fold, hind wing fold, abdominal anterior pocket, abdominal posterior pocket and hind tibal pocket (Grant 1978).

2.7.3.2 Perception of pheromones

An insect perceiving a pheromone is typically equipped with the physiological and morphological means for collecting molecule-bound information and translating it into the appropriate behavioural reaction. The pheromone perception of an insect is highly effective, enabling the detection of minute amounts of a pheromone, and of high selectivity to phase out the interference from other chemicals in the environment (Howse *et al.* 1998).

It is widely accepted that the antennae are the primary site for the detection of pheromones, particularly insect sex pheromones (Payne 1974; Agosta 1992; Schneider 1992). Kaissling (1971) provided a comprehensive account of insect antennae for several insect orders. Receptors have also been located on the maxillary and labial palps of some insect species but have limited use in pheromone perception (Seabrook 1978). The sensitivity of the antennae is determined by its' size and shape, and the number, location and type of the olfactory receptors on each. For example, *B. mori* has highly branched antennae, with areas up to 85mm^2, enabling the removal of a third of all pheromone molecules that pass over them (Howse *et al.* 1998). Sexual dimorphism is present in the antennae of many lepidopteran species. In some instances the female does not possess the sensillum required for pheromone reception (Albert & Seabrook 1973).

The antennae are perforated with a large number of pores through which the pheromone molecules diffuse via pore tubules into the lumen of the sensillum. This is commonly accepted as the first step of pheromone perception (Schneider 1992). The number of pores on each antenna ranges between the species examined, from 150 on a grasshoppers' sensillary peg (Jacobson 1972) to 50,000 on each sensillary hair of male *B. mori* (Howse *et al.* 1998). Generally, the number of molecules absorbed determines the effectiveness of the sensilla, and the size of the antennae reflects the number of sensilla present, i.e. catchment area of the antennae. Transduction occurs as the second step of pheromone perception, as the air-borne pheromone is transformed into a bioelectric response on the receptor neurons (Payne 1974). The understanding of transduction is incomplete, therefore the process has generated a great deal of interest, speculation and debate. Various hypotheses and models have been formulated (Stürckow 1970; Riddiford 1970; Kaissling 1971), however, the most substantiated are those reported by Schneider (1992).

2.7.4 Tortricid sex pheromones

Pheromones have been found in all phylogenetically higher families of Lepidoptera including the tortricid family (Jacobson 1972). As a result of the pest status of this family, tortricid moths have been used extensively in pheromonal research, resulting in the identification of over 60 sex pheromones and around 300 male attractants (Pherolist 2000; Arn 1991). The sex pheromones of tortricid species have been reviewed by many authors (Roelofs & Brown 1982; Arn 1991) and the following characteristics have been reported, with few exceptions. The pheromone components are composed of primary aliphatic alcohols, their corresponding acetates and aldehydes and contain 12 or 14 carbon atoms in a typically unbranched chain. The pheromones are typically unsaturated (*E* or *Z* configuration), in which one or two double bonds typically exist.

Roelofs and Brown (1982) provided a detailed review on tortricid sex pheromones and attractants, and indicated a connection between the sex pheromone components and the taxonomic position of the species. Further corroboration of this was provided by Horak *et al.* (1988). The three tortricid sub-families are characterised by the common occurrence of carbon chain length and the isomeric positioning. For example, the pheromones identified within the sub-family Tortricinae commonly exist as C_{14} structures and those within the sub-family Olethreutinae commonly exist as C_{12} structures. However, some exceptions do occur. Taxonomically related species often use blends of the same compounds, i.e. geometrical or positional isomers, but in characteristic proportions (Horak *et al.* 1988).

The key sex pheromone components within the sub-family Tortricinae, are (*Z*)–11- and (*E*)-11-tetradecenyl acetates (Tamaki 1985), and less widespread are the components (*Z*)-11- and (*Z*)-9-tetradecenyl acetates (Roelofs & Brown 1982). *Planotortrix excessana* has been identified as *Z*5-14:Ac and *Z*7-14:Ac (Foster & Dugdale 1988); and the pheromone for *E. postvittana* identified as *E*11-14:Ac and *E*9/E11-14:Ac (Bellas *et al.* 1983). Therefore, tetradecenyl acetates appear more widespread throughout this sub-family. According to Booig and Voerman (1984), the most widespread components found in the sex pheromones of the sub-family Olethreutinae are dodecen-1-ols and dodecen-1-ol acetates, with the double bonds occurring at the eighth or ninth positions. For example, the sex pheromone of *C. pomonella* has been identified as *E*8/*E*10-12:OH and 12:OH (Arn *et al.* 1985); and

the pheromone of *C. molesta* has been identified as *Z*8-12:Ac, *E*8-12:Ac and *Z*8-12:OH (Baker *et al.* 1981). Furthermore, Witzgall *et al.* (1996) found that within the tribes Eucosmini and Grapholitini sex pheromones and attractants were commonly found to contain the geometric isomers (*E*8, *E*10), (*Z*8, *E*10), and (*Z*8, *Z*10)-8, 10 dodecadien-1-yl acetate.

2.8 Conclusion

This review highlighted a variety of important biological and ecological factors of various tortricid species. Many of theses factors have proven vital in the development and implementation of pest management programs. The current research aims to explore the main issues raised with a tortricid pest that has become of increasing concern within eucalypt plantations in New Zealand, *Strepsicrates macropetana.*

3. General biology and rearing of *Strepsicrates macropetana*

3.1 Introduction

Strepsicrates macropetana has a phytophagous larval stage, causing damage to young *Eucalyptus* production plantations. This species is now established throughout Auckland, Northland, Bay of Plenty, Manawatu, Wellington and areas of the South Island, often reaching moderate pest status, however, no detailed biological studies have previously been reported. Based on recent forest health observations, it was decided that such research was imperative. This chapter provides the biological foundation required for subsequent research, and has the following objectives.

1. To ascertain basic life history parameters of *S. macropetana*.
2. To determine the most effective diet and method for rearing *S. macropetana*.
3. To determine the influence of *Eucalyptus* species on the life history of *S. macropetana*.
4. To investigate the host selection behaviour of female *S. macropetana*.

3.2 Life history

Nuttall (1985) provided the most recent account of *S. macropetana* life history. Detailed information regarding development stage durations, survival and fecundity was lacking. Therefore, work was required to investigate these parameters under laboratory conditions.

3.2.1 Materials and methods

Mature *S. macropetana* larvae were collected from *Eucalyptus nitens* and *E. fastigata* trees from a Tasman Forest Industries plantation in Kawerau, during November 1998 (refer to Chapter five for site information). Correct identification of *S. macropetana* was confirmed by W. Faulds (FRI, Rotorua, New Zealand) and M. Horak (CSIRO, Entomology, Canberra, Australia). A local supply (Old West Road, Palmerston North) of *Eucalyptus macarthurii* Deane & Maiden foliage was obtained and used as a larval host for *S. macropetana* in the current experiment. The current experiment was maintained at 20 ± 2°C, 60 - 70% RH, with a 16L: 8D photoperiod.

Two leaves were inserted into a glass stopper vial (5 x 1.5 cm) containing water. A paper towel square (2 x 2 mm) containing a single leafroller egg was adhered to one of the leaves with Blu tack®. The vial was then placed into an individual plastic container (10.1 x 8.5 cm; LabServ, Auckland) (n = 40), lined with filter paper (Whatman® 5.5 cm Ø) (Appendix 1). The foliage was replaced after consumed or when the leaves had lost turgidity and colour. The lid of each container was modified with a Tyvec™ paper (75gsm; the Paper House, New Zealand) covered hole (6 cm Ø).

Every second day age-dependent parameters such as development stage, integument colour, body length and head capsule width were recorded. Larval instar was determined by direct observation throughout the larval period, i.e. the presence or absence of exuviae. Head capsule width and body length measurements were made under a dissecting microscope (Nikon, x 10 eyepiece), with an eyepiece micrometer (μm) attached. Pupae were weighed with an electronic balance (Mettler AE 100; Watson Victor Ltd, New Zealand) and pupal length was obtained using a pair of Mitutoyo electronic callipers (Alanda Engineering Supplies Ltd, New Zealand). The pupae were sexed and placed as mating pairs into labelled plastic containers (10.1 x 8.5 cm) for mating and oviposition to occur (Appendix 1). The number of eggs that developed into adult stage was used as a measure of overall survival. A food source (5% sucrose solution) was dispensed through an inverted test tube (3 x 1.5 cm) containing a 25mm cotton wick (Richmond Dental Company, North Carolina, USA). An egg sheet (5 x 5 cm; paper towel; Ashby *et al.* 1985) was adhered to the inside wall of the container with Blu tack® and replaced when eggs were laid upon it. The total eggs laid were counted as a measure of fecundity. All eggs were held in numbered petri dishes (9 x 1.4 cm) for hatching to occur, enabling egg fertility to be measured. All significant dates (e.g. adult emergence and death) were also recorded.

A one-way analysis of variance (ANOVA) using Duncan's multiple comparative procedure was conducted to determine mean differences in head capsule width and body length between consecutive larval instars. Furthermore, two-sample t-tests were used to compare mean differences between male and female pupal weight and length, and adult longevity. The analysis was performed using SAS® Release v6.12 (SAS® Institute Inc. 1996).

3.2.2 Results

A full lifecycle of *S. macropetana* was completed within 54.1 ± 1.56 days (Mean ± SE) when developed on *E. macarthurii* (Fig. 3). Approximately half the total lifecycle (23.1 ± 1.26 days) was dedicated to larval development, with five larval instars evident. The development times, survival, fecundity and fertility obtained for *S. macropetana* are reported in section 3. 3. 2. 1.

The eggs of *S. macropetana* are ovoid in shape, with a flattened appearance, and have a width of 0.5 ± 0. 01 mm (Mean ± SE). When first oviposited, the eggs are cream in colour, changing to orange as the embryo develops. Prior to hatching, the black head capsule and translucent green body of the developing larva become visible. The eggs are oviposited either singly or in small irregular clusters of up to fifteen eggs.

Strepsicrates macropetana larvae develop through five larval instars. All instars have heavily sclerotized heads, differing in colour between instars. Each instar has three pairs of pale green segmented thoracic legs, and four pairs of unsegmented prolegs on the third to sixth abdominal segments, with a further pair evident on the tenth segment. The mean head capsule width and body length were significantly different between consecutive instars (F = 442.03; df = 4, 163; $P < 0.001$; F = 375.04; df = 4, 163; $P < 0.001$, respectively) (Table 2). However, the range of head capsule widths indicated a considerable degree of overlap between instars.

The first and second instars have a rounded black head capsule and prothoracic shield. The integument is translucent green on both the ventral and dorsal surfaces. Small sclerotized hooks (crochets) present on the prolegs are biordinal. The third and fourth instars both have a rounded light brown head capsule and prothoracic shield. The dorsal integument is medium green and exhibited pinnacula are set in white dots, containing imminent primary and subprimary dorsal setae. The anal shield is a consistent square shape containing a distinctive dark 'U' shape, only visible in later instars.

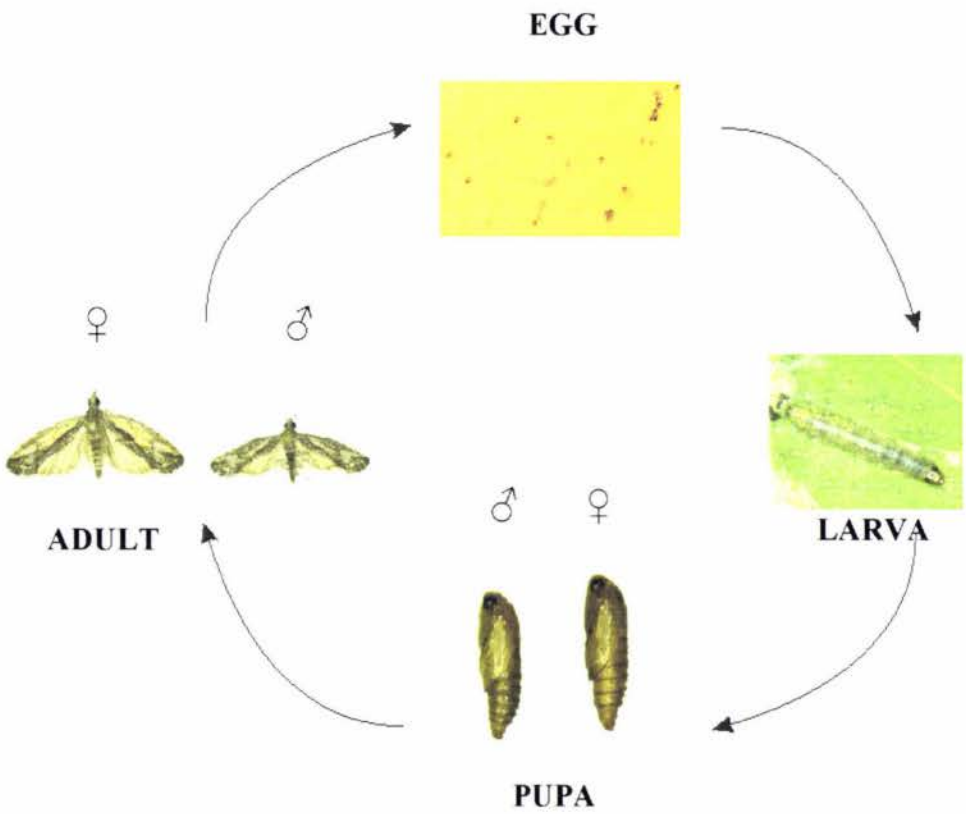

Fig. 3. The life-cycle of *Strepsicrates macropetana*.

The final instar exhibits a distinctive range of colour throughout its duration. The integument of the fifth instar larva is consistently pale green whilst feeding. However, feeding ceases close to pupation, after which the larva changes from its original colour, to pink/red, then brown. Following the location of a pupation site, the larva constructs a silken cocoon, subsequently contracting in size and moulting. The sex of the late instar larva can be determined by the presence (male) or absence (female) of darkened testes visible through the dorsal integument of the seventh abdominal segment.

Table 1. Characteristics of *Strepsicrates macropetana* larvae when reared on *Eucalyptus macarthurii* foliage (n = 38).

Instar	Head capsule width (mm)		Body length (mm)	
	Mean ± SE	Range	Mean ± SE	Range
L1	0.18 ± 0.005^{e}	0.15 - 0.25	1.61 ± 0.05^{e}	0.80 - 2.20
L2	0.28 ± 0.013^{d}	0.15 - 0.46	2.96 ± 0.12^{d}	1.80 - 4.50
L3	0.53 ± 0.025^{c}	0.35 - 0.70	5.50 ± 0.26^{c}	3.10 - 8.90
L4	0.86 ± 0.028^{b}	0.62 - 1.10	8.43 ± 0.26^{b}	6.04 - 11.30
L5	1.13 ± 0.020^{a}	0.91 - 1.32	11.18 ± 0.25^{a}	8.96 - 13.50

*In the same column, means accompanied by different letters are significantly different at $P < 0.05$.

Pupation of *S. macropetana* occurs within a protective silk cocoon, which is typically adhered to dried leaf material or against other dry substrate (filter paper, netting). The pupae are golden brown in colour and gradually darken closer to adult emergence. The pupae are adecticous, with all appendages fused to the body wall (obtect). Two rows of spines are visible on the dorsal side of each abdominal segment, including the terminal. The terminal segment in both male and female consists of several fused abdominal segments. These segments contain the anus and genital openings, with the position of such varying with gender. Sexual dimorphism is also evident by the number of movable abdominal segments present; the male pupa has four movable segments, whilst the female has three. A cremaster is absent from the terminal segment, however, the segment bears a number of hook-shaped hairs. Female pupae are significantly heavier than males ($t = 2.1$; $df = 9, 15$; $P < 0.05$) (Table 3). However, there was no difference in the length of female and male pupa (7.08 ± 0.16 vs 7.13 ± 0.22 mm, respectively; Mean = SE), ($t = 0.17$; $df = 9, 15$; $P > 0.1$).

The hind wings of both male and female are uniform brown grey in colour, and are fringed with scales (Figs 4 & 5). The forewing is broadly triangular in shape, with a rounded termen. The distal part of the costa has a succession of irregular dark oblique lines, and three short longitudinal lines (ocellus) present just above the termen. The wingspan was between 12 and 16 *mm*, with the wings held roofwise when rested. This species shows sexual dimorphism in forewing colouration, with the male having relatively uniform ash/grey fore wings, and the female having a lighter wavy band across the costa, edged by a thin darkened line. The male forewing also has a fringe of scales along the termen, furthermore scales containing sex pheromone producing structures are suspected within a fold along the basal part of the costa (See Chapter five). The antennae are filiform, reaching to the middle of the forewing when rested. The male antenna has a prominent notch just up from the basal segment. Male and female can also be distinguished by their external genitalia. The female's anus and ovipore are situated on the periphery of the large papillae anales within the terminal segment, whereas the male has a large pair of claspers visible. Overall, females live significantly longer than males (16 ± 1.16 vs. 12.5 ± 0.92 days (Mean ± SE), respectively). ($t = 2.5$, $df = 9, 14$; $P < 0.05$)

3.2.3 Discussion

The results indicate that a complete life-cycle of *S. macropetana* consists of four main developmental stages (egg, larva, pupa and adult), of which the feeding larval stage constitutes nearly half of the total life-cycle. *Strepsicrates macropetana* develops through five larval instars. In accordance with Horak (1991), most tortricid species have five or six larval instars. The transition between larval instar is typically measured by the width of the head capsule, generally, with each instar represented by a distinguishing head capsule width. The degree of overlap between the consecutive instars of *S. macropetana* suggests that head capsule width alone is not conclusive for differentiating instars. Schmidt *et al.* (1977) found that the measurement of head capsule width was erroneous due to development polymorphism and other factors that can occur under laboratory conditions. Although the mean capsule widths of *S. macropetana* are significantly different, the wide range of capsule width occurring in each instar indicates that such a method is not useful for instar identification. Therefore, mean head capsule widths used in combination with the larval descriptions presented above will give a more accurate account of instar identification.

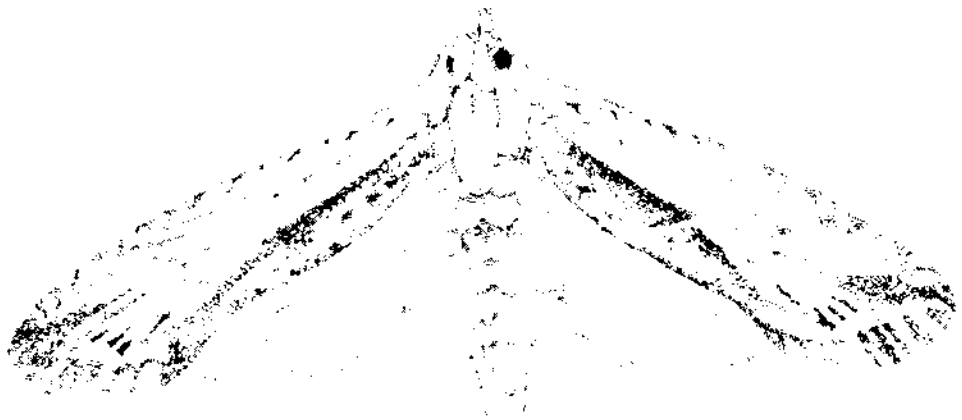

Fig. 4. Female *Strepsicrates macropetana*.

Fig. 5. Male *Strepsicrates macropetana*.

The life history parameters recorded for *S. macropetana* were similar to other species within the same genus. *Strepsicrates rhothia* Meyrick, a pest of several plant species including *Eucalyptus* and guava (*Psidium guajava* L.), has an average development time of 44 ± 2 days, and a maximum fecundity of 43 eggs, under laboratory conditions (Ahmad 1962). *Strepsicrates ejectana* (Walker) has morphological traits similar to those of *S. macropetana*, with comparable body size, and colouration at the larval and adult stages (Braza 1991).

Certain unique features can aid in the identification of *S. macropetana* in the field. The larva of this species can be identified from other leafrollers by the presence of green segmented and unsegmented legs, as these are darkened in many leafroller species. The later instars of *S. macropetana* have a square shaped anal shield incorporating a "U" shaped mark and have distinguishing white spots on the integument. Such features are not found on other species of leafroller within New Zealand. The adult of *S. macropetana* can be identified by wing colouration, as irregular dark lines, and three short longitudinal lines can be seen on the forewing of both male and female. Additionally, a light wavy band along the costal margin of the female forewing is further feature not present in other species of leafroller.

3.3 The effect of diet and rearing method on development

To regularly obtain a sufficient number of experimental insects, a study was undertaken to determine the most optimal food source for larval development and the most efficient method of rearing *S. macropetana*. This objective was achieved by a comparison between natural diet and an artificial food source, and the application of these on a large scale i.e. mass rearing. Many tortricid species have been reared using an artificial diet, making it possible to obtain several generations a year within the laboratory (Singh 1985). Rearing of *S. macropetana* has been attempted with general-purpose diet (GPD) in the past, with the rate of survival unknown (Singh 1977). The following experiments were undertaken in attempt to replicate this process.

3.3.1 Materials and methods

3.3.1.1 Individual rearing with *Eucalyptus* foliage and GPD

Strepsicrates macropetana were reared on the foliage of young *E. saligna* trees, and general purpose diet (GPD). Forty-eight young *E. saligna* trees were donated by Forest

Research (Rotorua, New Zealand), in December 1998. A further fifty trees were purchased from the Pioneer Nursery (Colyton, Fielding), in April 1999. The eucalypts were initially grown in pots (12.5 x 16 cm) and were re-potted (25 x 25 cm) when approximately 75 cm tall into Dalton's nursery media (consisting of pH mix, can fines, fibre, pumice, dolomite, aypsum, lime), and additionally pg mix, osmocote and general purpose water soluble fertilizer (Peters® Professional, Scotts Australia Pty Ltd, New Zealand) were added to the mix. The trees were watered with a hand held hose as required. The young trees were grown and maintained within a glasshouse at the Plant Growth Unit, Massey University (Palmerston North), with a natural photoperiod, and ambient temperatures ranging between 9 - 25°C, with ambient humidity.

General-purpose diet (GPD) was obtained from the Horticulture and Food Research Institute of New Zealand Limited (Mt. Albert Research Centre, Auckland), made in accordance with the GPD recipe (Singh 1984; Appendix 2). Forty plastic test tubes (7.5 x 1 cm) containing GDP (3 x 1 cm) were randomly assigned to a wooden rack (38 x 9 x 4.5 cm). Each tube was inoculated with a paper towel square (2 x 2 mm) containing a *S. macropetana* egg and was plugged with a 25 mm cotton wick. Larval, pupal and adult parameters were collected as in section 3. 2. 1

The parameters collected in the previous section (3. 2) were used to compare the life history parameters of *S. macropetana* reared on *Eucalyptus* foliage and GPD. Data were analysed as in section 3. 2. 1, providing comparison between the overall duration, larval duration, development stage duration, and pupal weight. The data obtained from examining pupal period, fecundity and fertility were log transformed due to a skewed distribution. The number of insects that survived from egg to adult was used as a measure of overall survival and was displayed graphically.

3.3.1.2 Mass rearing with *Eucalyptus* foliage and GPD

Mass rearing of *S. macropetana* with *Eucalyptus* foliage was undertaken in a large plastic container (38 x 12 x 25 cm; New Ocean, New Zealand). The container was modified with two holes (10 x 10 cm) in the lid and four holes (5 x 5 cm) within the walls of the container. Tyvec™ paper (75 gsm) was adhered to the holes with glue, to permit ventilation. Newly hatched larvae (n = 40) were inoculated onto fresh foliage with a fine tipped paintbrush. Fresh *E. saligna* foliage was replaced every three days with that from young trees

Prior to inoculation, bulk GDP was conditioned at 20°C for 24hr to evaporate any excess moisture (Ashby *et al.* 1985). The GPD was then cut into eight cubes (2.5 cm^3) and placed inside a plastic container (22 x 5 x 16 cm). The lid contained a series of small holes (2.5 x 2.5 cm) that were covered with Tyvec™ paper. Neonate larvae ($n = 40$) were inoculated onto the diet using a fine tipped paintbrush, at a density of five individuals per diet cube. The diet was checked once a week for dryness or mould and was replaced if required. Pupal and adult parameters were collected and the data analysed as in section 3. 2. 1, from which a comparison was made between survival, overall developmental time, pupal period, pupal weight, longevity, fecundity and fertility. Data from pupal period, fecundity and fertility were log transformed.

3.3.2 Results

3.3.2.1 Individual rearing with *Eucalyptus* foliage and GPD

The effects of diet on *S. macropetana* life history parameters are presented in Table 3. *Strepsicrates macropetana* reared with *Eucalyptus* foliage developed significantly faster ($t = -4.0$; $df = 2, 25$; $P < 0.01$), with a significantly shorter larval development time ($t = -3.0$; $df = 2, 25$; $P < 0.05$) than when reared on GPD. Pupal duration was also significantly shorter when reared with *Eucalyptus* foliage ($t = 3.2$; $df = 2, 25$, $P < 0.01$), with the pupal weights of larvae reared on *Eucalyptus* foliage significantly heavier than those reared on GPD ($t = 2.8$, $df = 2, 25$; $P < 0.05$).

The survival of *S. macropetana* from egg to adult was 62.5% and 7.5%, when reared with *Eucalyptus* foliage and GPD, respectively (Fig. 6), therefore obtaining a significant difference ($L = 31.374$; $df = 1$, $P < 0.0001$). The greatest mortality occurred throughout the first, second and third larval instars from those reared on GPD, with the majority of deaths occurring within the first instar (50%). However, when reared on *Eucalyptus* foliage the highest mortality occurred during the fourth instar (15%). Overall, the greatest mortality occurred throughout the larval period, with the least occurring from the pupal to adult period.

3.3.2.2 Mass rearing of with *Eucalyptus* foliage and GPD

The overall development time of *S. macropetana* was not significantly different from rearing with the two diets ($t = 0.2$; $df = 1, 22$; $P > 0.1$). However, larval development period was significantly different, with larvae reared on GPD taking longer to develop ($t = -6.2$; $df = 1, 25$; $P < 0.05$).

Table 2. The development duration (days), pupal weight (mg), fecundity and fertility (number of eggs hatched per female) of *Strepsicrates macropetana* when reared individually on *Eucalyptus* foliage and general-purpose diet (GPD).

	E. macarthurii (n = 40)		GPD (n = 40)	
Parameters	Mean ± SE	Range	Mean ± SE	Range
Egg period	6.9 ± 0.13 *	5 - 8	7.9 ± 0.16*	6 - 10
1st larval instar	2.9 ± 0.19 *	2 - 6	5.6 ± 0.54*	2 - 14
2nd larval instar	4.8 ± 0.45	2 - 15	5.6 ± 0.53	2 - 11
3rd larval instar	4.1 ± 0.29 *	2 - 7	7.2 ± 0.84*	4 - 14
4th larval instar	4.8 ± 0.42	2 - 13	4.5 ± 1.45	2 - 7
5th larval instar	6.5 ± 0.55	3 - 13	5.3 ± 1.33	4 - 8
Pupal period	9.9 ± 0.27 *	7 - 13	13.6 ± 1.21*	12 - 16
Pupal weight (F)	1.58 ± 0.05*	1.07 - 1.76	1.28 ± 0.22*	1.02 - 1.54
Pupal weight (M)	1.38 ± 0.09*	1.03 - 2.02	1.24 ± 0.15*	1.12 - 1.37
Adult longevity	14.3 ± 0.94	5 - 25	10.3 ± 2.02	7 - 14
Total life span	54.1 ± 1.56 *	41 - 65	62.0 ± 1.73*	59 - 65
Total survival	62.5%*	-	7.5%*	-
Fecundity	40.0* (45.6)	0 - 125	0* (0)	0
Fertility	27.6* (37.5)	0 - 124	0* (0)	0

† In the same row, means accompanied by * are significantly different at $P < 0.05$

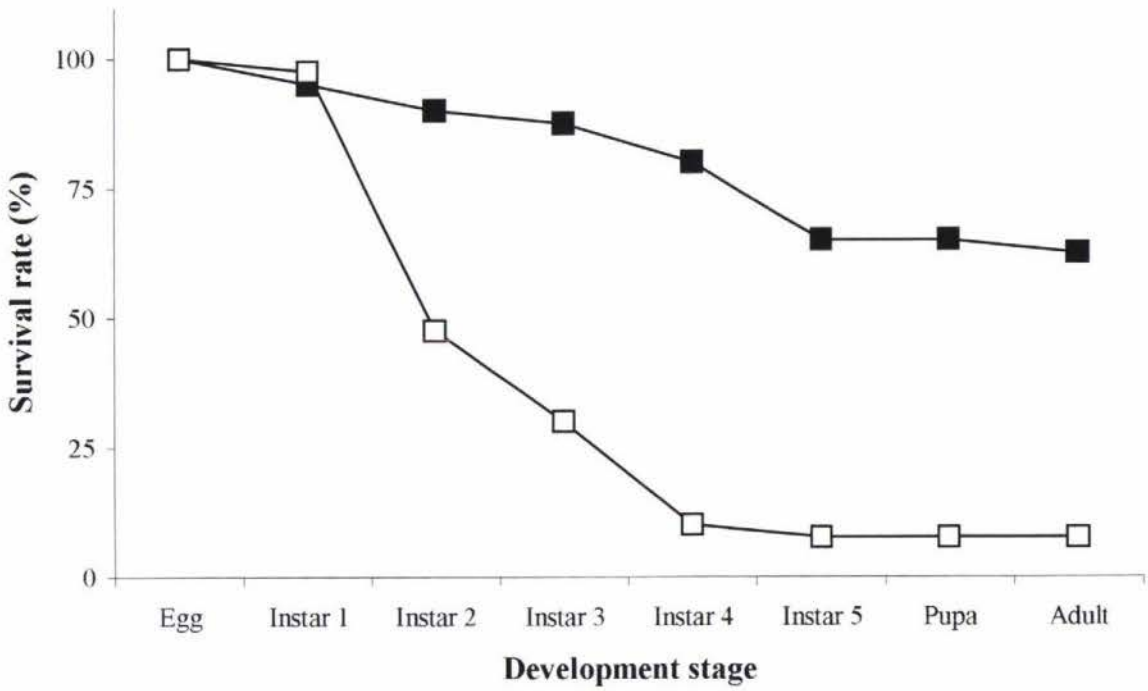

Fig. 6. The survival of *Strepsicrates macropetana* when individually reared on *Eucalyptus* foliage (■) and general-purpose diet (□).

Pupal duration was significantly shorter (t = -2.2; df = 1, 25; $P < 0.05$) and weight considerably heavier when larvae were reared with *Eucalyptus* foliage (t = 2.6; df = 1, 25; $P < 0.01$). Adult longevity of the individuals reared on *Eucalyptus* foliage was significantly greater (t = 8.3, df = 1, 22; $P < 0.001$) than those that developed on GPD. The fertility of *S. macropetana* was dependent on diet, as those reared with *Eucalyptus* foliage produced significantly more fertile eggs than those reared on GPD (t = 2.3; df = 6, 27; $P < 0.05$). The overall survival of those reared on *Eucalyptus* foliage was 57.5%, compared to 5% when reared on GPD.

3.3.2.3 Discussion

The current study indicated that rearing with *Eucalyptus* foliage was best for colony maintenance, even on a large scale. This was evident as a shorter larval period, pupal duration, heavier pupa, and greater fertility and survival of adults were obtained for those developed on eucalypt foliage in comparison to those developed with GPD. When the codling moth was reared on a natural diet of immature apple and on an artificial diet similar results were obtained. Those reared with an apple diet had shorter development times, heavier pupae, and greater rate of survival. However, no differences were apparent in longevity, fecundity and fertility (Hathaway *et al.* 1971). Other leafroller species examined also developed slower on artificial diet (e.g. Tomkins *et al.* 1989). Various factors influence food intake, including nutritional suitability, the presence of phagostimulants, deterrents, and other physical factors (Benz 1991). The greatest success with rearing insects on artificial diet has been found when the diet was customised to the nutritional requirements of the insect and when larvae were in the final instars before inoculation (Benz 1991). Howell (1970) found no negative effect was apparent on development time, fecundity or fertility when rearing *Cydia pomonella* (L.), if the artificial diet was modified to suit the species. Artificial diets used for some lepidopteran rearing typically have little or no connection to the preferred food plant of the insect, such as the diets used to rear many tortricid species, e.g. *Argyrotaenia velutinana* (Walker) and *Cydia molesta* (Busck). The success of such a diet is often greatest when the species are polyphagous and do not require specific feeding stimulants. Therefore, the use of generalised diets for oligophagous species, such as *S. macropetana* may be limited. The development of a more nutritionally specific artificial diet is required for *S. macropetana,* so that the diet is more suitable to the nutritional and phagostimulatory needs of the larvae. This may eliminate the need for a fresh foliage rearing method.

3.4 The resulting method for rearing

Results of the above experiment (3. 3. 2) indicated that a *Eucalyptus* diet was optimal for the rearing of *S. macropetana*. However, further refinements were required to develop a more efficient method, as maintaining foliage freshness was a limiting factor. Therefore, the methodology was modified to achieve a more effective rearing method.

3.4.1 Materials and methods

A wooden framed cage was built with the following dimensions, 125 height x 75 width x 75 cm length (Appendix 3). The wooden floor was covered with a layer of white plastic for protection. Three walls and the door were made from transparent perspex. Fine wire mesh was used to cover the roof, back wall and side vents, as leafrollers do not oviposit upon such surfaces (Tomkins *et al.* 1991a). The mesh enabled sufficient airflow within the cage. Between four and six young *Eucalyptus* trees (~90 cm height) were kept in the cage at all times, providing sufficient oviposition and feeding sites, and the trees were watered as required. The cage was maintained in a glasshouse with a natural photoperiod, ambient temperatures ranging between 9 - 25°C, and with ambient humidity, using the insects collected in section 3. 2. 1 as a founder population. Every two months, the plants were removed from the rearing cage. Any larvae still present were transferred onto undamaged trees with a fine tipped paintbrush, and then placed into the cleaned rearing cage. Pupae (80%) were harvested and the remaining 20% were retained within the cage, enabling the development of a further generation. A second larval collection occurred in the Bay of Plenty (Kawerau) early June 1999, to augment the *S. macropetana* colony. After the first generation, information including number of pupae, male and female pupal weights, and the sex ratio obtained, was collected to give an indication of colony success.

3.4.2 Results

After the first generation, 287 pupae were harvested from the rearing cage, of which a 4M: 3F sex ratio was obtained. The average pupal weight of female and male obtained was 1.51 ± 0.07 and 1.37 ± 0.05 mg, respectively (Mean ± SE). As a result a sustainable and efficient colony was established.

3.4.3 Discussion

The results gave a clear indication that *Eucalyptus* foliage was an optimal food source for rearing *S. macropetana.* As a result, *Eucalyptus* foliage was utilised in the resulting method. Additionally, rearing in a larger container was more desirable as it produced more insects with less human intervention. These results were taken into account, in order to refine the methodology. Ultimately, a method was derived that proved less time-consuming and enabled the development of a self-maintaining colony.

3.5 The effects of host plant on development

It has been demonstrated that the species of host plant used for larval development may have a significant impact on the life history traits of an insect (Smirle 1993; Danthanarayana 1975; Barrington *et. al* 1993; Tomkins *et al.* 1989). Therefore, as an extension to previous sections, a study was performed to determine if the species of *Eucalyptus* has an influence on the life history of *S. macropetana.*

3.5.1 Materials and methods

Four economically important *Eucalyptus* plantation species, *E. saligna, E. fastigata, E. nitens,* and *E. regnans,* were utilised in the current experiment. Ten trees of each species were purchased from Matatoa Nurseries (Shannon) in December 1998 and were maintained within a glasshouse as in section 3. 3. 1. The experiment had a complete randomised block design (CRBD). Each block contained eight cylindrical hang nets, with two trees of the same species present under each, resulting in four replications of each *Eucalyptus* species (Fig. 5). The hang nets (150 cm height, 100 cm Ø) were constructed from curtain netting, and contained a wire hoop (100 cm Ø) at the top and bottom for structural reinforcement (Fig. 6). The nets were suspended from wire hooks (50 cm length) attached to a horizontal over-wire (200 cm above the bench top). Each tree was inoculated with fifteen eggs, obtained from the *S. macropetana* colony. Once at pupal stage, the insects were collected, and pupal and adult parameters were collected as in section 3. 2. 1. Fecundity and fertility data were log transformed due to a skewed data set. A one-way analysis of variance (ANOVA) was performed to obtain a comparison of pupal weight, development time, fecundity and fertility between individuals reared on the different eucalypt species. Additionally, the significance of means was tested using the Duncan's multiple comparative procedure. A measure of survival was obtained as in section 3. 2. 1, i.e. number of individuals developing from egg to adult. Based on statistical separation, the life history parameters of

S. macropetana were scored so that a species ranking could be obtained. The ranking identified the range of host suitability for *S. macropetana*. Highest ranking (most suitable) was assigned to the characteristics of heaviest pupa, shortest life span, highest fecundity and fertility, and the highest survival.

3.5.2 Results

The results indicated that larvae developed on *E. fastigata* had significantly lighter pupae weight compared to those developed on other *Eucalyptus* species ($F = 5.1$; $df = 3, 315$; $P < 0.001$; Table 3). The overall mean development time was significantly shorter for those developed on *E. nitens* than on *E. regnans* ($F = 2.59$; $df = 3, 234$; $P < 0.05$). *Eucalyptus fastigata* was the host on which *S. macropetana* showed the highest survival, with 57% of larvae reaching the adult stage. Whereas, *E. saligna* was the poorest host for survival, with only 26% of larvae reaching the adult stage. Overall, the greatest mortality occurred during the larval stages, with lowest mortality occurring throughout the pupal stage. Females that developed on *E. regnans* laid significantly more eggs, than those developed on *E. saligna*, *E. fastigata* and *E. nitens* ($F = 2.89$; $df = 3, 130$; $P < 0.05$). Furthermore, egg fertility was significantly higher with the individuals developed on *E. regnans* ($F = 2.16$; $df = 3, 103$; $P < 0.05$).

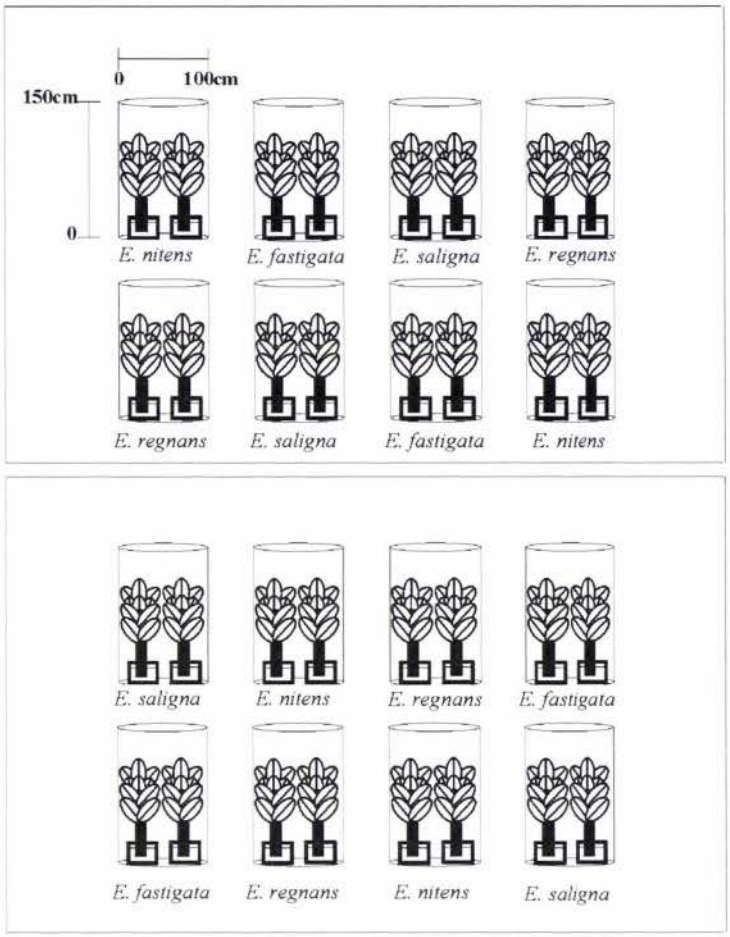

Fig. 7. The experimental layout for detecting the effects of *Eucalyptus* host species on *Strepsicrates macropetana* development.

Fig. 8. The cylindrical hang nets used to contain eucalypts and *Strepsicrates macropetana*.

Table 3. The influence of *Eucalyptus* species on the pupal weight (mg) and development duration (days) of *Strepsicrates macropetana*.

	E. fastigata		*E. regnans*		*E. nitens*		*E. saligna*	
Parameters	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Pupal weight	1.47 ± 0.03 [b]	0.72 – 2.15	1.60 ± 0.03[a]	0.90-2.21	1.62 – 0.03[a]	1.13 – 2.36	1.62 ± 0.05[a]	0.75 – 2.37
Pupal period	12.4 ± 0.03 [a]	7 - 20	12.6 ± 0.29 [a]	6 - 18	10.7 ± 0.38 [b]	6 - 18	12.5 ± 0.34 [a]	6 - 18
Adult longevity	28.7 ± 1.17 [a]	6 - 47	31.1 ± 1.16 [a]	7 - 52	28.3 ± 1.08 [a]	13 - 47	28.9 ± 1.42 [a]	11 - 44
‡Total life span	70.1 ± 1.23 [ab]	49 - 93	72.7 ± 1.11 [a]	54 - 94	67.9 ± 1.15 [b]	52 - 88	70.5 ± 1.43[ab]	53 - 86
Total survival	57%	-	54%	-	48%	-	26%	-
Fecundity	33.9 ± 6.91[ba]	0 - 270	63.9 ± 10.14[a]	0 - 252	31.8 ± 7.73[b]	0 - 197	37.9 ± 10.0[ba]	0 - 240
Fertility	22.0 ± 6.06[b]	0 - 270	54.7 ± 10.13[a]	0 - 249	25.7 ± 7.13[b]	0 - 197	24.2 ± 2.46[b]	0 - 232

†Within a row, means accompanied by different letters are significantly different at $P < 0.05$, using Duncan's multiple comparative procedure.
‡Total duration (days) of the egg, larval stages 1-5, pupa and adult.

Based on the parameters below (Table 4), the larvae of *S. macropetana* developed on *E. nitens* and *E. regnans* achieved the best scores (scores of 8 and 9, respectively), whereas those developed with *E. fastigata* and *E. saligna* were ranked lower (both scores of 11).

Table 4. Ranked life history parameters of *Strepsicrates macropetana*.

Species	Pupal weight (mg)	Pupal period (days)	Life span (days)	Fecundity	Survival
E. nitens	1	1	1	4	1
E. regnans	1	2	4	1	1
E. saligna	1	2	2	2	4
E. fastigata	4	2	2	2	1

3.5.3 Discussion

The present study confirmed that the *Eucalyptus* species used for development affected the developmental parameters of *S. macropetana*. It can be seen that *E. nitens* and *E. regnans* were the most suitable species for larval development, together giving the highest pupal weight, shortest pupal period, overall shortest lifespan, and the greatest fecundity. No single host species was consistently worse or better than the other for all life stage measurements, indicating no obvious advantage. Previous studies have used such parameters to examine tortricid health and determine the influence of host species. In accordance with Delisle and Hardy (1997), the species of larval host plant used by the male tortricid *Choristoneura fumiferana* significantly influenced the reproductive success of both sexes, i.e. fecundity. Similar results were found by Carriere (1992), in which the fecundity of *Choristoneura rosaceana* increased by 26% when larvae developed on apple leaves. The overall poor result of those developed on *E. saligna* in the current study could be related to the health of the trees growing in pots rather than a true representation of health when developed on this species in the field. Further studies would be required to confirm this speculation.

The nutritional content of a host plant can influence the uptake of food in most insect species. Any variation in these factors will manifest itself in the development

parameters of the insect. Behmer and Grebenok (1998) found that differences in phytosterol structure can have pronounced effects on life history traits of *Plutella xylostella* (L.). *Eucalyptus* foliage typically contains low levels of nitrogen and high concentrations of secondary compounds such as tannins, other phenols and essential oils. So far it has been found that only the nitrogen concentration has an effect on larval performance. For example, *Paropsis atomaria* (Ol.) requires a threshold of nitrogen to be exceeded for optimal development to occur (Ohmart & Edwards 1991). The physical factors of eucalypts have also been found to effect herbivory, such factors include leaf toughness (Ohmart & Edwards 1991) and the presence of leaf waxes (Edwards 1982).

The development times obtained for *S. macropetana* within the current section were substantiality longer than for those developed on the foliage of *E. macarthurii* (Section 3.2). In the former situation, the environmental conditions were uncontrolled within glasshouse conditions. Whereas in the latter, the environmental conditions were controlled, therefore without the occurrence of environmental fluctuation. Furthermore, the species of eucalypt, as seen in the present experiment, may have had an effect on the development time of the insect, with the effect being more pronounced in a glasshouse situation.

3.6 Female host plant selection

The interactions between a herbivorous insect and its host plants are extremely diverse, with selection involving the use of various synergistic stimuli (Hodkinson & Hughes 1982). The maintenance of a herbivore/host plant relationship and the evolution of new relationships are dependent on the insect's ability to use appropriate stimuli to trigger corresponding reactions.

Many *Eucalyptus* species have proven unsuitable for production within New Zealand, particularly due to their pest and pathogen vulnerability (Nicholas & Hay 1989). Therefore, knowledge of the factors regulating host selection for key *Eucalyptus* insect pests could further assist in selecting and enhancing the current species grown, and the possible re-establishment of previously unsuitable species within New Zealand. The objective of the current study was to provide information regarding the stimuli utilised for host selection and the ovipositional preference of female *S. macropetana*.

3.6.1 Materials and methods

The experimental arena utilised for examining host selection consisted of a wooden frame (40 x 65 x 40 cm) and floor, perspex roof and door, and fine cotton mesh walls (Fig. 9). Shoots of five plant species were contained within the arena, of which four were known hosts of *S. macropetana* (*Eucalyptus fastigata*, *E. regnans*, juvenile *E. nitens* and *E. saligna*) (shoots sourced from section 3.2) and one non-host, apple (cv. Fuji). Apple shoots were obtained from local trees in Palmerston North. Each shoot had approximately sixty leaves, and was of similar age and health. The shoots were inserted into separate paper sealed containers (Tyvec™; 75gsm), each containing water to prolong shoot turgidity.

Male (n = 100) and female (n = 100) pupae were held separately in net cages (30 x 30 x 30 cm), and supplied with a food source upon emergence (see section 3.2). Three days after emergence, twenty virgin adults (M10: F10) were randomly assigned to and released within the experimental arena. Six days after release, the number of eggs laid on each plant species; the eggs laid on other surfaces; the total number of leaves laid upon; and the number of eggs positioned on the lower, upper and stem surfaces and along the mid-vein or between veins were recorded. The experiment was replicated ten times, with the position of each plant species in the arena randomised between replicates. The experiment was conducted at 20 ± 2°C, 60 – 70% RH, within a 16L: 8D photoperiod.

For the purposes of the current study the term 'mid-vein' has been used to describe the primary vein running vertically through the centre of the leaf. In addition, the term 'between-vein' has been used to describe any position on a leaf where leaf veins, either primary or secondary are not present. A log data transformation was performed on all data before analysis. The total eggs laid on each species were analysed to compare the attributes given above (eggs laid on each plant species and on other surfaces, the number of leaves laid upon, and the number of eggs laid on the lower, upper and stem surfaces and along the mid-vein or between veins) using an ANOVA and the Duncan's multiple comparative procedure. Due to differences between the experimental replicates, blocking effects were incorporating into the ANOVA, to remove any covariance created.

3.6.2 Results

A comparison was made of eggs laid on the eucalypt species, those laid on apple, and those laid on cage surfaces within the arena. The results indicated a significant difference, with most eggs laid on eucalypt foliage ($F = 6.34$; $df = 2, 30$; $P < 0.001$). The number of leaves of each species receiving eggs was examined. The statistics showed a significant difference between the *Eucalyptus* species and non-host species examined ($F = 10.53$; $df = 4, 31$; $P < 0.0001$), with the leaves of *E. regnans* receiving the greatest number of eggs, than of any other species examined (Fig. 10).

The preference for plant part as a substrate for oviposition was examined for all the species. There was a significant difference in oviposition, independent of host plant, with a preference shown for the lower leaf surface ($F = 18.12$; $df = 2, 27$; $P < 0.001$). *Strepsicrates macropetana* oviposited significantly more eggs on the lower leaf surface of *E. fastigata* and *E. regnans* (Table 5). However, there was no such difference detected in oviposition between *E. saligna*, *E. nitens* and apple foliage. The placement of eggs on the lower and upper leaf surface were further examined by arbitrarily separating the leaf into two areas, i.e. mid-vein and between veins. A greater number of eggs were received along the mid-vein area of the leaf surface when ovipositing on *E. fastigata*, *E. saligna* and *E. regnans*. Overall, there was a significant difference apparent in where eggs were deposited ($F = 23.41$; $df = 4, 78$; $P < 0.0001$; Table 5). Egg deposition appeared to be more random on *E. nitens* and apple foliage, with no significant preference for the mid-vein area or between the vein area.

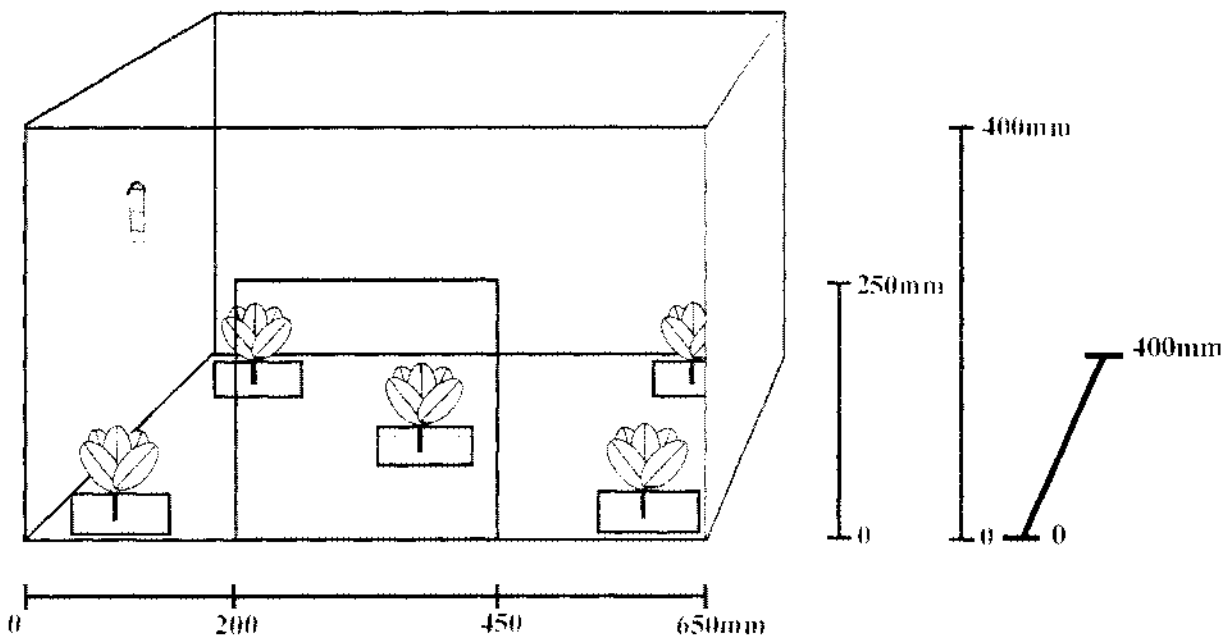

Fig. 9. Host selection arena used to assess *Strepsicrates macropetana* oviposition preferences.

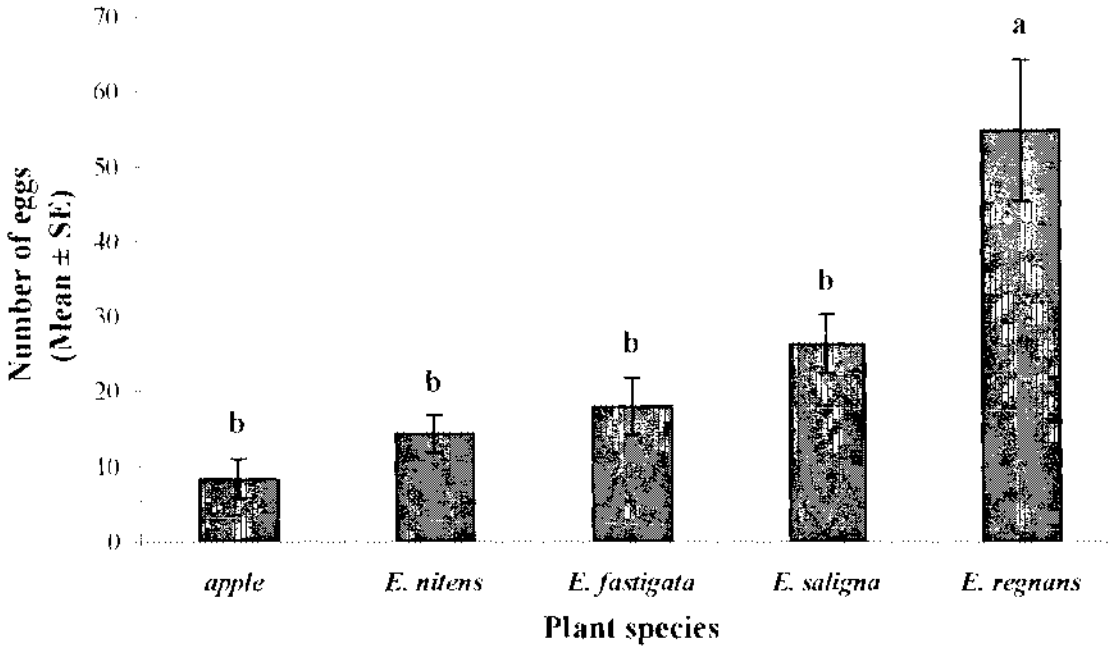

Fig. 10. The oviposition of *Strepsicrates macropetana* on non-host and host plants in a choice test. Means accompanied by different letters are significantly different at $P < 0.05$.

Table 5. Oviposition of *Strepsicrates macropetana* on host vs. non-host foliage when enclosed in a choice arena.

	Number of eggs laid			Location of eggs	
Plant species	Lower leaf (Mean±SE)	Upper leaf (Mean±SE)	Stem (Mean±SE)	Mid-vein (Mean±SE)	Between veins (Mean±SE)
E. fastigata	12.3 ± 3.8^{a}	4.8 ± 1.5^{b}	1.0 ± 1.0^{b}	14.8 ± 3.5^{a}	2.3 ± 0.7^{b}
E. saligna	15.7 ± 3.0^{a}	10.3 ± 2.1^{a}	0.4 ± 0.4^{b}	20.5 ± 3.1^{a}	6.1 ± 1.0^{b}
E. regnans	34.2 ± 6.9^{a}	20.3 ± 3.5^{b}	0.4 ± 0.3^{c}	50.2 ± 8.7^{a}	4.7 ± 1.0^{b}
E. nitens	5.4 ± 1.4^{a}	8.3 ± 1.9^{a}	0.7 ± 0.4^{b}	7.3 ± 1.9^{a}	6.5 ± 1.3^{a}
Apple	3.4 ± 1.1^{a}	5.0 ± 1.5^{a}	0^{b}	4.7 ± 1.6^{a}	3.7 ± 1.3^{a}

†Treatment means within a row followed by the same letter are not significantly different at $P < 0.05$, using Duncan's multiple comparative procedure.

3.6.3 Discussion

The host finding and acceptance behaviour of a herbivorous insect is mediated by the presence or absence of positive stimuli from potential host plants (Prokopy & Owens 1983). *Strepsicrates macropetana* expressed a strong preference for ovipositing on *Eucalyptus* foliage, indicating that close range stimuli emitted by the foliage exceeded the critical motivational threshold for oviposition (Courtney *et al.* 1989). All *Eucalyptus* species examined in the current study showed variation in their acceptability for oviposition by *S. macropetana*. *Eucalyptus regnans* was most preferred, with *E. saligna*, *E. fastigata*, and juvenile *E. nitens*, descending in order of acceptability. This infers that a conceptual ranking may exist in the preference of *Eucalyptus* for oviposition by female *S. macropetana*. Many authors recognise that female oviposition is hierarchical when confronted with an array of potential hosts on which to lay eggs, i.e. the hierarchy-threshold model (Courtney *et al.* 1989). Considering that some moths oviposit indiscriminately in caged tests (Withers & Barton Browne 1998), it is likely that in the field environment preference for certain *Eucalyptus* hosts would be even stronger.

It is widely recognised that olfactory and tactile stimuli are important for the host selection of nocturnal insects (Prokopy & Owens 1983). However, further experimentation is required to confirm this with *S. macropetana*. Tactile stimuli inherent in the plant species examined appeared to be important in egg placement. *Eucalyptus regnans* was most suitable for oviposition by *S. macropetana*. Young *E. regnans* shoots are very supple, concolorous in nature and contain minimal epicuticular wax in comparison to eucalypts from the southern blue-gum group. *Eucalyptus nitens* was the least preferred eucalypt species for oviposition. The juvenile leaves of *E. nitens* are opposite in appearance and are covered by a glaucous wax layer. Many advantages have been attributed to such a leaf surface, including insect and frost resistance, and water repellency (Edwards 1982). Edwards (1982) demonstrated that the wax layer present on juvenile *E. nitens* foliage provided protection against the grazing of *Paropsis charybdis* (Stål), as the insect was unable to obtain a sufficient foothold.

Tactile characteristics of the plant appeared to have been involved in the positioning of *S. macropetana* eggs. Oviposition occurred most frequently on the abaxial (lower) leaf surface rather than the adaxial (upper) surface and stem of the plant. Differences in abaxial and adaxial cuticular lipids, texture, pubescence, and microclimate effects may be responsible for oviposition site preferences. The codling moth (*Cydia pomonella* (L.)) laid more eggs on the abaxial surface of stone fruit (Curtis *et al.* 1990). In contract, a preference was shown for the adaxial surface of apple leaves by Plourde *et al.* (1985), due to the degree of pubescence, as high densities of hair deterred oviposition. The tortricid *Epiphyas postvittana* showed preference for smoother adaxial surfaces, with deprivation of a smooth surface resulting in reduced fecundity (Foster & Howard 1999).

The oviposition of *S. macropetana* was most common along the mid-vein of the leaf in the majority of plant species examined. The influence of a prominent leaf mid-vein on the selection of oviposition site has been recorded in many insect species. For example, oviposition of *E. postvittana* was significantly increased by the presence of a prominent mid-vein or synthetic wax ridge (Foster *et al.* 1997).

It is possible that the limitations of the current study may have influenced the results. The controlled size of the arena possibly distorted host selection, resulting in

competition and interference from other females and conspecific males. As noted by Withers and Barton Browne (1998) indiscriminate oviposition in host specificity tests can be linked to the physical characteristics of the arena. In addition, length of exposure of *S. macropetana* to the potential host plants may have influenced the outcome, either by delaying the response or enabling associative learning. In the future, the use of a larger arena and a shorter time frame may avoid such problems.

An understanding of biological processes, including host selection, can provide a means for developing alternative, non-chemical methods for managing pests. For example, the use of visual and chemical stimuli in trap development, use of resistant cultivars, and improved site selection. *Strepsicrates macropetana* demonstrated a strong preference for ovipositing along the mid-vein area of a concolorous leaf, therefore future planting of *Eucalyptus* species without these strong characteristics could be beneficial, as a change in preferred stimuli could possibly disrupt an essential process of host selection.

4. Phenology, abundance and natural enemies of *Strepsicrates macropetana*

4.1 Introduction

Strepsicrates macropetana is regarded as an oligophagous pest of *Eucalyptus*, in which feeding prevalence has been noted on a number of species within the genus (Nuttall 1983; Mauchline *et al.* 1999). Defoliation of eucalypts by *S. macropetana* is intermittently severe, possibly related to factors such as season, tree growth and natural enemy abundance. It had been reported that *S. macropetana* has at least two generations per year in the field (Nuttall 1983). Laboratory studies indicated a life of about 70 days under ambient temperatures, which would suggest the number of generations per year should be much greater than two. Therefore, the objectives of this chapter were to determine the number of generations *S. macropetana* completes each year in the field, the abundance of *S. macropetana* on different eucalypt species, and the effect of season on these parameters. Furthermore, data on the presence, identity and abundance of any natural enemies were to be obtained.

4.2 Materials and methods

Investigations were undertaken over a 12-month period (Jan 1999 to Dec 1999), in which a population of *S. macropetana* was monitored fortnightly. Without prior knowledge of the species or the effectiveness of the technique devised, it was expected that monitoring would be an iterative process. Sites were preferentially selected on the basis of the eucalypt species, and tree age (up to five years). It was not possible to find suitability located sites which shared both of these factors.

Observation and monitoring of *S. macropetana* was carried out within five commercial and farmer owned plantations (Table 6). To avoid sampling bias and collecting samples from an unrepresentative area, each site was divided into four replicates, each of which contained the same number of trees and tree species in each. A minimum of thirty minutes was spent at each replicate, from which approximately ten percent of the trees in each were monitored to ensure acceptable representation. Each tree was scanned for leafroller damage from top to bottom (or from wherever foliage was within sight) on each of four sides. Active leaf rolls were easily distinguished by their colour, and were discernible from those constructed by other leafroller species by the position and formation of the leaf roll. An indication of the larval instars present

was achieved by randomly opening leaf rolls. Approximately five leaf rolls were opened for each tree, however the number was dependent on density. The presence of an egg, pupa, or adult was similarly determined by scanning surfaces such as leaf upper and lower, tree trunk, and the periphery and base of each tree, searching for the presence of these life stages. Direct counting was achievable for these life stages due to limited sighting. The regular sampling undertaken at sites two, three and four (Table 6) made it possible to assign development stages to a generation based on maturity, and therefore, estimate the number of generations occurring per year.

Table 6. Study site summary.

Site	Site location	Trees planted	Year planted	Trees sampled	*Eucalyptus* species
1	Hogg Road, Kawerau, Bay of Plenty	10,000	1997	55	*E. nitens* *E. fastigata*
2	Old West Road, Manawatu	400	1998	209	*E. brookerana* A. M. Gray *E. macarthurii*
3	Massey Sheep and Beef Farm - Tuapaka, Manawatu	1008	1995	154	*E. nitens*, *E. saligna*, *E. botryoides*, *E. obliqua*, *E. regnans*, *E. agglomerata* Maiden, *E. cladocalyx* F. Muell, *E. pilularis* J. Sm., *E. microcorys* F. Muell, *E. baxteri* (Benth.) J. M. Blakely, *E. muelleriana* Howitt, and *E. globoidea* Blakely
4	Feilding, Manawatu	151	1998	197	*E. nitens*
5	Kimbolton, Manawatu	70	1997	89	*E. nitens*

To open every leaf roll on a tree proved very difficult and time consuming. The scale below was used to approximate the number of leaf rolls per tree, therefore enabling an approximation of abundance to be obtained over time, site, eucalypt species and season. The number of active leaf rolls produced by *S. macropetana* on each tree sampled was estimated, and then translated into the appropriate score.

- 0 = absent
- 1 = scarce (1-5 leaf rolls per tree)
- 2 = moderate (6-10 leaf rolls per tree)
- 3 = abundant (11-20 leaf rolls per tree)
- 4 = severe (20+ leaf rolls per tree)

Further data collected at each study site included sampling date, and eucalypt species present. Approximately five (number collected dependent on abundance) late instar (4-5) larvae or pupae and foliage from the eucalypt species in which the larvae were obtained, were randomly collected at each site and brought back to the laboratory to pupate in transparent plastic containers (10.1 x 8.5 cm). Pupal weights, sex ratio, fecundity and parasitism rate were determined for the field populations, the former being derived as in section 3. 2. 1. Healthy pupae were placed together as a mating pair and supplied with an egg sheet and a sucrose solution (10%) on emergence. Any eggs laid were counted, and placed in numbered petri dishes (9 cm Ø) for hatching. Females were dissected after death to ascertain the remaining number of discernible eggs, so potential fecundity could be determined (potential fecundity was the sum of eggs laid and remaining un-laid eggs). Furthermore, any natural enemies were identified upon emergence, with the proportion of infected insects determined for each sample, enabling the parasitism rate of any natural enemies to be approximated. Percentage parasitism was defined as (number of parasitoids emerged/total leafrollers collected) x 100.

A collation of observations made in the field was reported. Mean abundance of *S. macropetana* was calculated on a per tree basis. Data were checked for normality. A multiple ANOVA was performed to examine the effects of host species and site on pupal weight. A multiple ANOVA was also undertaken to examine the effects of host species and site on potential fecundity. Once site effects were eliminated then a non-parametric Mann-Whitney test was used for separating median values to detect any difference in the potential fecundity of adult females after larval development on different eucalypt species. A multiple ANOVA was performed to detect any differences in *S. macropetana* abundance according to the species of eucalypt, different study sites and climatical variation. The differences between means were separated using a Duncan procedure. Finally, a multiple ANOVA was performed to detect the factors influencing the abundance of *S. macropetana* when developed on *E. nitens*, as it was the most representative of the eucalypt species across multiple sites.

4.3 Results

4.3.1 General observations from the field

Eggs were commonly found laid singly on the underside of a leaf and positioned next to a vein or at the junction of two veins. After hatching, neonate larvae would typically move a short distance from the egg case before feeding commenced, with which abrasions were made in the leaf surface, also typical of the damage produced by younger larvae (2-3rd instars). Older larval instars (4-5th) more commonly constructed leaf rolls from foliage and silken threads, feeding within the resultant shelter. A larva feeding within a leaf roll would eject frass produced out of the rear of the roll and the exuviae from previous moults would be pushed out of the front of the roll. Younger larvae were often found within leaf rolls constructed and abandoned by older instars. Furthermore, more than one ($\leq$ eight) young larva was occasionally found to inhabit the same leaf roll.

Observation suggested that younger larvae had a preference for the young, suppler foliage, and were commonly observed on the shoot tips and leaf buds of young trees. Older larvae were observed on both the young growth and leaves lower down the tree. Overall, larvae preferentially fed on the younger leaves, shoot tips and leaf buds of the tree. On those species in which the leaves are opposite rather than alternate (e.g. juvenile *E. nitens* and *E. brookerana*), early instar larvae were commonly found in webbing created at the base or junction of the two juvenile leaves. Furthermore, where adult foliage was present, no feeding of *S. macropetana* was observed, however, other species of leafroller were observed feeding.

Larvae of other leafroller species were most commonly observed on mature leaves throughout the lower proportion of the tree. Therefore, due to a change in appearance, feeding damage was easily distinguishable between the various species of leafroller present. *Strepsicrates macropetana* larvae were more commonly observed feeding on the shoot tips of those eucalypt species with tougher leaves, e.g. *E. macarthurii*, and were less commonly found on the shoot tips of those species with more supple leaves, e.g. *E. brookerana*. There was no evidence of a diapausal stage, but it was observed that larvae developed more slowly under cooler conditions, where less response to touch and movement was also evident. Pupae and adults were found infrequently throughout the year, due to their cryptic nature. Most pupae were observed in crevices on or below the tree, e.g. within bark, soil and old leaves. Adults were most commonly found

resting on leaves, particularly on those partially damaged, on which they were well camouflaged. Adults were more evident on clear, fine days and were occasionally observed feeding on liquid droplets on the surface of eucalypt leaves. No courtship or mating behaviour was seen throughout the field observations at the study sites.

Many other insect species were observed during the present study, including representatives from most insect orders. The most common species observed were *Opodiphthera eucalypti* (Scott) (Emperor gum moth), *Paropsis charybdis* Stål (*Eucalyptus* tortoise beetle), *Ophelimus eucalypti* (Maidenaria) (Gahan) (gall wasp), *Phylacteophaga froggatti* Riek (leaf blister sawfly), *Ctenarytaina eucalypti* (Maskell) (blue gum psyllid), as well as various other Lepidoptera, arachnids, Hymenoptera, Diptera and possible predatory species.

4.3.2 Phenology and abundance

Larvae collected from the field revealed a range of pupal weights for *S. macropetana*. The model from the multiple ANOVA showed a moderate fit in predicting the variation ($r^2 = 0.68$), with weight significantly explained by site ($F = 67.77$; $df = 3, 233$; $P < 0.0001$), and by eucalypt species ($F = 59.53$; $df = 6, 233$; $P < 0.0001$). Those larvae collected from *E. microcorys* and *E. macarthurii* had the highest average weight, and those from *E. saligna* had a significantly lower weight (Table 7). Larvae collected from *E. botryoides* and *E. saligna* did not survive to adult stage due to parasitism and other undetermined factors.

Table 7. Pupal weights and the potential fecundity of field-collected *Strepsicrates macropetana*.

Eucalypt species	Number collected	Weight (mg) (Mean ± SE)	Potential fecundity (Mean ± SE)
E. microcorys	20	1.89 ± 0.04 [a]	62.50 ± 6.00
E. macarthurii	21	1.83 ± 0.02 [a]	74.00 ± 4.76
E. brookerana	43	1.78 ± 0.01 [a]	147.25 ± 2.88
E. nitens	72	1.72 ± 0.003 [a]	98.07 ± 1.19
E. fastigata	62	1.71 ± 0.01 [a]	116.33 ± 2.77
E. botryoides	11	1.58 ± 0.09 [a]	NA
E. saligna	13	0.91 ± 0.03 [b]	NA

† NA indicates no specimens survived to adult stage

‡Means accompanied by different letters were significantly different at $P < 0.001$.

Field populations of *S. macropetana* revealed a sex ratio of 1:1. Random representatives collected throughout the 1999 period indicated a slight male bias when developed on *E. macarthurii* and *E. nitens*, where the ratio was 1.25: 1 and 1.27:1, respectively. Potential fecundity was significantly greater when *S. macropetana* larvae were developed on *E. brookerana* under field conditions ($F = 2.37$; $df = 4$; $P < 0.01$). Whereas larvae developed on *Eucalyptus microcorys* had the lowest potential fecundity, although sampling showed that *E. microcorys* supported the highest larval abundance in the field. Those adult females that had developed on *E. brookerana* and *E. microcorys* laid the most eggs. Those adult females that had developed on *E. fastigata* and *E. nitens* laid a similar number of eggs, but when un-laid eggs were taken into account, the potential fecundity was higher for those developed on *E. fastigata* (Table 7)

The abundance of early instar larvae peaked throughout February (Fig. 11), subsequent to a peak in late instar larvae throughout March. Throughout the months of July, October and December, early as well as older larval instars peaked simultaneously, suggesting an overlap in generations. The abundance of eggs, pupae and adults were too variable to assist with phenology calculations. A rapid increase in combined early and late instar larval abundance throughout March suggests that a new generation (autumn generation) occurred at this time (Fig. 12). Further peaks in larval abundance were observed in July, October and December indicating the likelihood of additional generations (winter, spring and summer generations). Its appears that one generation was completed every 60 days in the summer season, with generations taking around 90 days under cooler temperatures. From the examination of such evidence, it was concluded that the total number of *S. macropetana* generations in the Manawatu and Bay of plenty regions throughout the 1998/1999 12 month period equated to at least four, however, the overlap evident in the summer suggests the possibility of a further generation occurring during this time (Fig. 12).

A multiple ANOVA was carried out on abundance. The model showed a moderate fit in prediction of the variation ($r^2 = 0.62$), with abundance significantly explained by host species ($F = 20.50$; $df = 14, 675$; $P < 0.0001$), and by temperature ($F = 73.20$; $df = 11, 675$; $P < 0.0001$), but with no effect of site ($F = 1.50$; $df = 3, 675$; $P < 0.57$). The decline in abundance between April and June coincided with a relatively consistent decrease in temperature, indicating that such environmental conditions were integral in the influence of *S. macropetana* phenology. Furthermore, the decline in

abundance throughout August and September was coincidental with low ambient temperatures (Appendix 4), with the lowest monthly temperatures during the year in both the Bay of Plenty and Manawatu regions (Fig. 12). However, it was also evident that temperatures throughout July were low while abundance remained high, presumably as the autumn generation fed, prior to pupating.

A greater abundance of *S. macropetana* was evident at sites one, two, and five throughout the 1999 period. During March, the abundance of *S. macropetana* at sites two and four increased, and throughout July, October and December abundance increased again at all sites. Similar trends evident within the Manawatu sites indicated that abundance estimates obtained were representative of *S. macropetana* phenology within the region (Fig. 13).

The abundance of *S. macropetana* was significantly influenced by the *Eucalyptus* species on which they were found (Fig. 14). *Strepsicrates macropetana* was most frequently observed on *E. microcorys, E. fastigata, E. brookerana* and *E. nitens*, whereas, low abundance was recorded on *E. pilularis* and *E. obliqua.* Due to the lack of reproducible sites, certain eucalypt species including *E. microcorys* and *E. brookerana* were only present at one site. Therefore, such a trend is dependent on the factors (e.g. elevation, wind velocity, exposure) specific to each site. *Eucalyptus agglomerata, E. baxteri* and *E. globoidea, E. muelleriana, E. nitens, E. pilularis*, and *E. regnans* supported unexpectedly high levels of abundance during autumn. *Eucalyptus fastigata,* and *E. macarthurii* had similar levels of *S. macropetana* abundance across all seasons. *Eucalyptus brookerana, E. botryoides, E. cladocalyx* and *E. saligna* supported higher abundance levels in the spring and summer seasons, with fairly moderate levels otherwise. *Eucalyptus obliqua* showed only low levels of leafroller abundance throughout all seasons, whereas *E. microcorys* supported higher levels of abundance in the summer season.

Eucalyptus nitens was present at more than one site, so a multiple ANOVA was also carried out on abundance. The model showed a moderate fit to predicting the variation ($r^2 = 0.57$), with abundance significantly explained by site ($F = 13.02$; $df = 3, 318$; $P < 0.0001$), and significantly by temperature ($F = 34.44$; $df = 11, 318$; $P < 0.0001$). Higher temperatures resulted in significantly greater abundance of *S. macropetana* during those sampling periods.

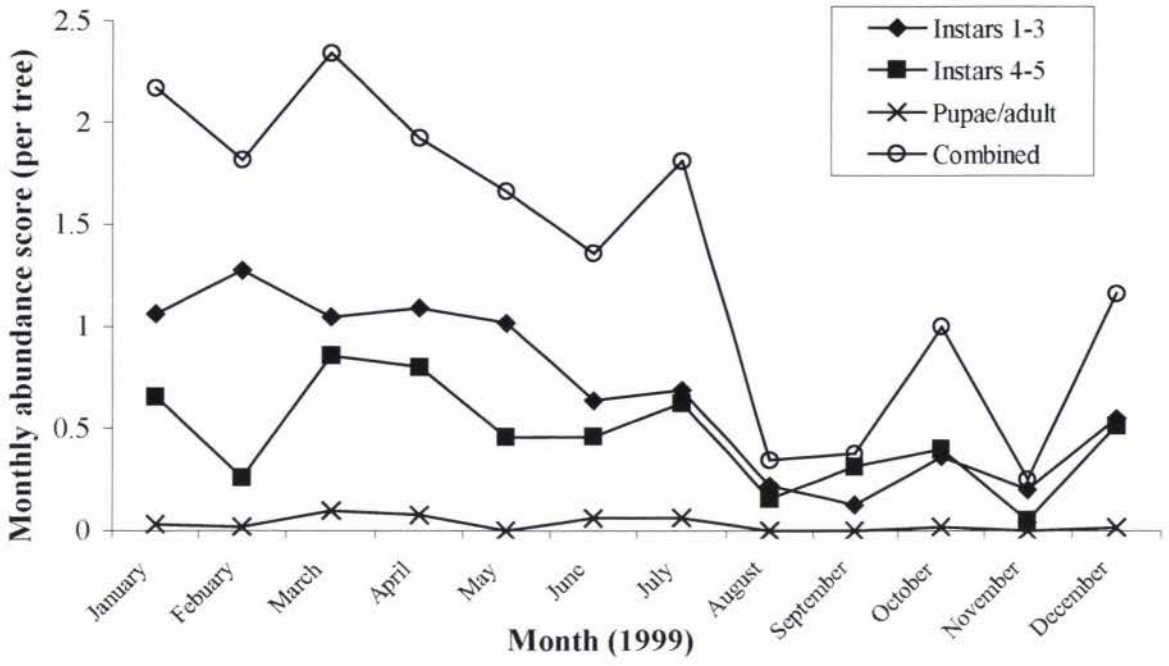

Fig. 11. Combined abundance of *Strepsicrates macropetana* development stages throughout the 1999 period across all study sites.

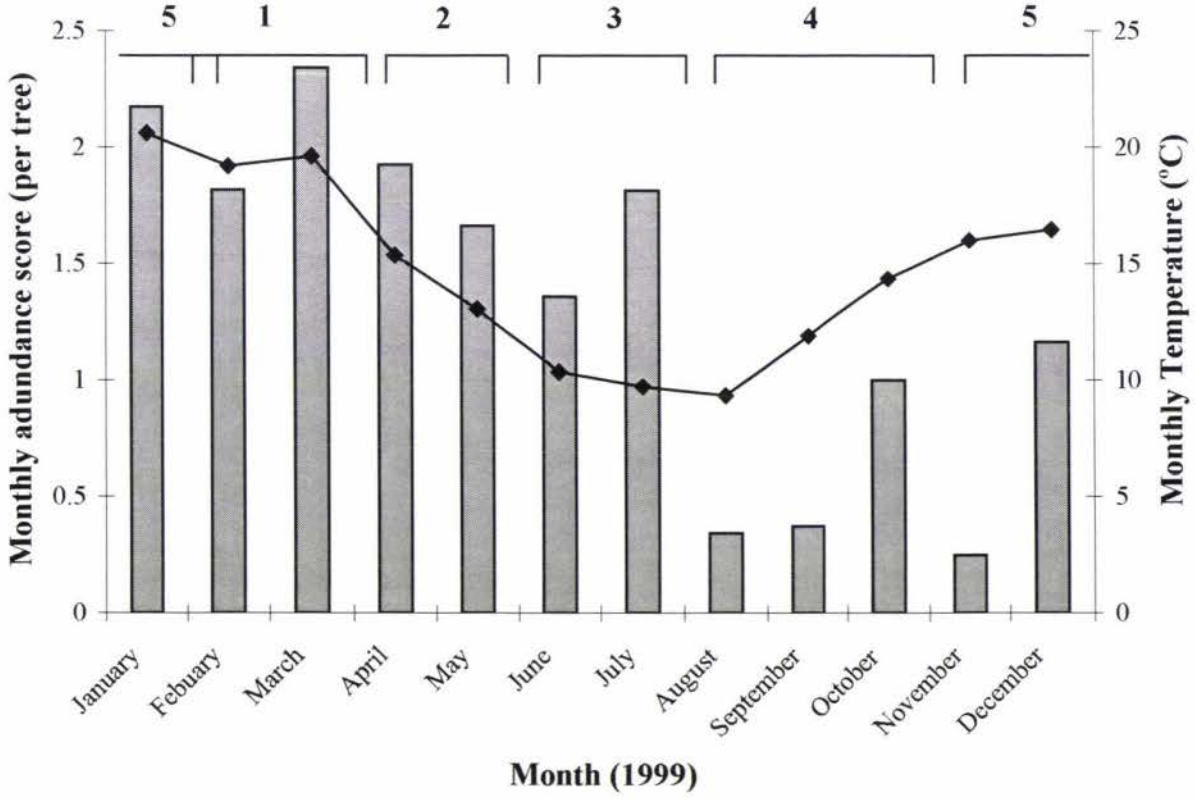

Fig. 12. The monthly abundance of *Strepsicrates macropetana* (column) combined across all sites, and corresponding ambient temperature (line) throughout the 1999 period. Numbers (1-5) represent the generations of *S. macropetana* identified.

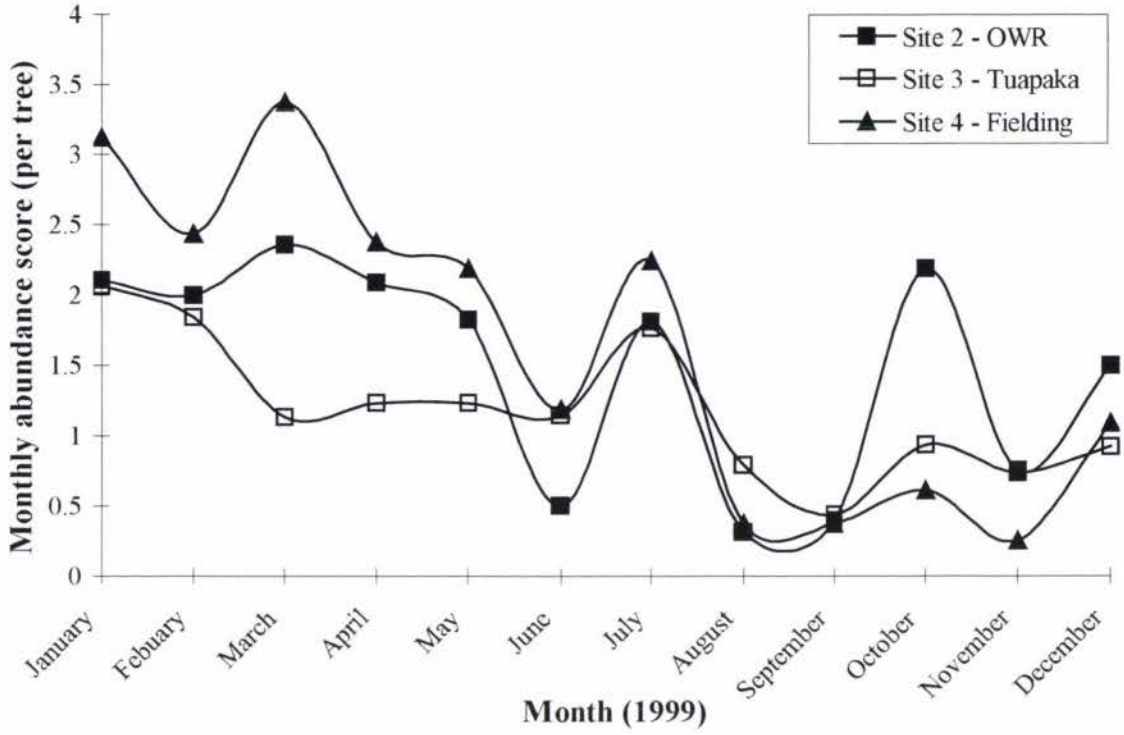

Fig. 13. The monthly abundance of *Strepsicrates macropetana* at three sites within the Manawatu region.

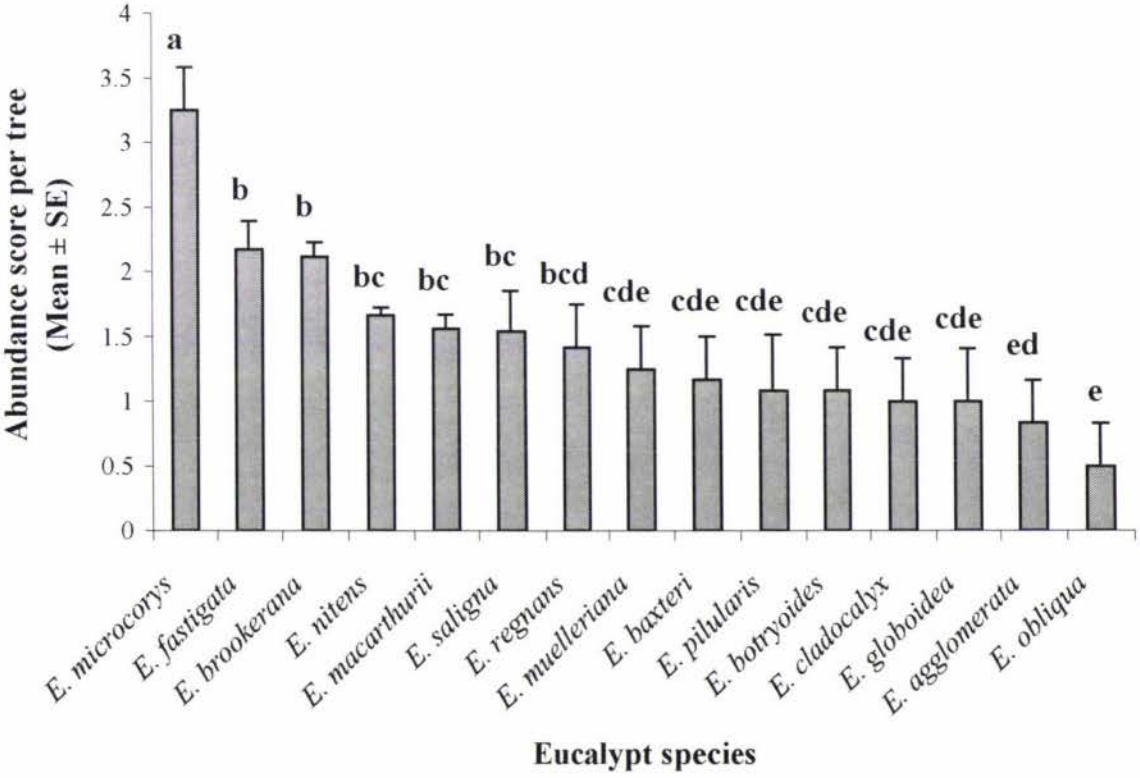

Fig. 14. The mean abundance estimate of *Strepsicrates macropetana* on fifteen eucalypt species combined across all sites and all seasons. Means accompanied by different letters were significantly different as $P < 0.05$.

4.3.3 Natural enemies

Natural enemies of *S. macropetana* have been observed in both the Bay of Plenty and Manawatu regions. *Trigonospila brevifacies* (Diptera: Tachinidae) (specimens identified by V. Munroe) was frequently observed parasitising late instar larvae of *S. macropetana*. Larvae were seen to receive up to six white, cylindrical eggs (0.5mm) of *Trigonospila brevifacies* on their prothoracic shield and thoracic segments, which hatched as *S. macropetana* reached pre-pupa or pupal stage. Parasitised pupae of *S. macropetana* were darker in colour and appeared round and swollen (Fig. 15). Adult parasitoids were observed throughout most of the year, typically associated with leaf rolls or observed resting on foliage. Voucher specimens of *T. brevifacies* have been deposited in the National Forest Insect Collection, Forest Research, Rotorua, New Zealand.

Trigonospila brevifacies was identified as the primary natural enemy of *S. macropetana* in the current study, dominating the parasitoid complex with parasitism rates as high as 45%. Parasitism by *Trigonospila brevifacies* indicated three peaks in abundance throughout the 1999 period; the most substantial being the increase throughout June and July at sites one and two, respectively. Such parasitism was preceded by a relatively low abundance of *S. macropetana* throughout August and September (Fig. 16).

The literature claims that an unidentified protozoan is the predominant natural enemy of *S. macropetana* (Nuttall 1983). However, the current research has not provided any evidence to support this. On one occasion larvae were found dead and desiccated inside a leaf shelter but the low incidence did not indicate high mortality. No adult predators, parasites or pathogens were observed during this study. However, predation is highly likely given the number of insect predators present at most sites, e.g. an unidentified neuropteran, various arachnid species, earwigs and praying mantids.

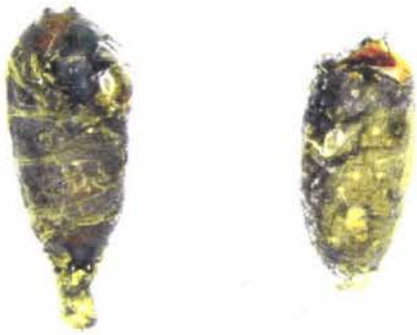

Fig. 15. ***Strepsicrates macropetana*** **pupae parasitised by** ***Trigonospila brevifacies.***

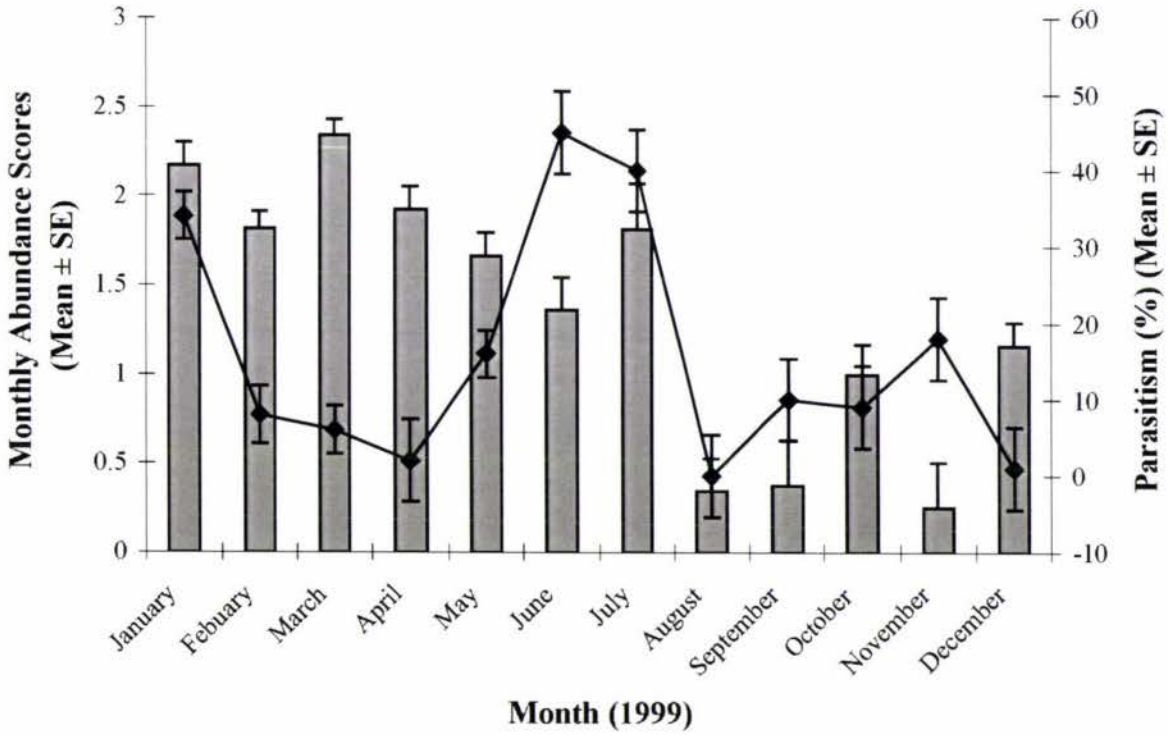

Fig. 16. Mean parasitism by ***Trigonospila brevifacies*** **(line) and the mean abundance of** ***Strepsicrates macropetana*** **throughout the 1999 period (column) summarised across all sites.**

4.4 Discussion

4.4.1 Phenology and abundance

Four to five generations of *S. macropetana* were identified throughout the 1999 period, these coinciding with the autumn, winter, spring and summer seasons. The overall abundance of *S. macropetana* was influenced by the presence of suitable host plants, the climatic conditions evident, and in some instances site conditions. Shaw *et al.* (1994) found that host plant and environmental conditions had a significant effect on the distribution and abundance of native leafrollers in New Zealand. The same conclusion can be drawn on the abundance of *S. macropetana* in New Zealand.

The trends identified for *S. macropetana* indicate a significant variation in abundance between eucalypt species. The highest abundance recorded in this study was on *Eucalyptus microcorys* and *E. brookerana*, particularly during the summer season. However, these hosts were only present at one site. Considering other sites and seasons, *E. agglomerata, E. baxteri, E. globoidea E. muelleriana, E. nitens, E. pilularis*, and *E. regnans* also carried a relatively high abundance of *S. macropetana*.

Ecological, physiological or chemical variation may be present in the eucalypt species between seasons. For example, differences in microclimate, wind velocity, wind gradient, rainfall, and leaf chemistry. As found by Danthanarayana (1975), variation in the fecundity of *E. postvittana* has been attributed to larval food plant, temperature, and larval crowding, with more eggs laid when larvae were developed on preferred host plants and under cool conditions. Female *E. postvittana* adults found in summer produced significantly fewer eggs than those of the spring and autumn generations, due to the cooler conditions preferred for oviposition. No detailed study regarding the ecological requirements of *S. macropetana* was undertaken, and little information of this type exists.

Differences in host plant physiology and chemistry may have affected the abundance of *S. macropetana*. The hypothesis that climatic variation can affect the nutritive value of the host-plant was confirmed through experimentation with the tortricid *Choristoneura occidentalis*. It was found that such variation could bring on a 25% difference in the reproductive rate of females (Campbell 1989). As stated by Casotti and Bradley (1991), the distribution of eucalypt insects has been strongly influenced by the foliar nitrogen content within the leaves. Eucalypts are typically low

in nitrogen, therefore, insects have to consume a greater quantity to obtain sufficient quantities of nitrogen. Many insects occurring on eucalypts have developed mechanisms that permit the efficient assimilation of nitrogen. For example, Edwards and Wightman (1984) demonstrated that *Paropsis charybdis* was able to assimilate approximately 59% of the nitrogen contained within the foliage of *E. viminalis*, which has a nitrogen content of only 2.33%. It is possible that insect species lacking such efficient assimilation mechanisms may tend to occur on eucalypt species whose foliage contains higher nitrogen content. Furthermore, younger leaves and shoot tips contain higher nitrogen content and larvae preferentially fed within this region on some hosts.

Other factors may also affect the abundance of insects on eucalypts. In accordance with Ohmart and Edwards (1991), eucalypts have evolved various secondary defence chemicals constituting up to 5% of the leaf dry weight, and varying significantly between species of eucalypts. Younger leaves and shoot tips are believed to contain higher tannin levels (Larson & Ohmart 1988). As this is typically where *S. macropetana* prefers to feed, this implies that this tortricid has either evolved a mechanism to detoxify such compounds or the ability to limit its distribution to species with lower levels of secondary compounds. The factors mentioned above, together with inherent biological variation, most likely influence the abundance and distribution of *S. macropetana*.

4.4.2 Natural enemies

The current study found that *T. brevifacies* was the most abundant natural enemy of *S. macropetana* in the Bay of Plenty and the Manawatu regions. This was not the first significant recording of this parasitoid. Berry (1990) noted that *T. brevifacies* was the most dominant tachinid parasitoid within the complex contributing to the control of *Heliostibes atychioides*.

High parasitism of *S. macropetana* by *T. brevifacies* was observed in June and July at sites one and two within the current study. Abundance of this natural enemy had earlier been predicted to be lower at this time due to the seasonal regulatory factors evident. Furthermore, a high variation in parasitism rates between the data sets indicates the possibility of other factors influencing the populations of *S. macropetana*.

Trigonospila brevifacies was introduced into New Zealand from Australia between 1976 and 1973 (Thomas 1975), and subsequently in 1981 and 1982 (Russell 1987), as a biological control agent for tortricid orchard pests. It has since been recorded parasitising three tortricid hosts within New Zealand, including *Ctenopseustis obliquana* (Walker), *Epiphyas postvittana* and *Cnephasia jactatana* (Green 1984). Rearing has also been attempted on a number of tortricid non-hosts including the pterophorids *Platyptilia falcatalis* Walker and *Aciptilia monospilalis* Walker; the oecophorid *Heliostibes atychioides* (Butler); the stathmopodid *Stathmopodid skelloni* (Butler); the geometrid *Pasiphila lunata* (Philpott); and an unidentified psychid (Green 1984).

Two other parasitoids are also known to have an association with *S. macropetana.* The pupal parasitoid *Xanthopimpla rhopaloceros* (Krieger) (Hymenoptera: Ichneumonidae) was observed hunting around shelters of *S. macropetana* in Gisborne (J. Clearwater, pers. comm.). Additionally an egg parasitoid identified as *Trichogrammatoidae bactrae* Nagaraja (Hymenoptera: Trichogrammatidae), was observed to have emerged from an egg of *S. macropetana* (T. Withers, pers. comm.) (specimen identified by J. Berry). These natural enemies were not located in any of the study sites within the current study.

Xanthopimpla rhopaloceros was introduced from Australia in 1976 and again in 1969, also as an attempt to control orchard pests, particularly *Epiphyas postvittana*. It is now established in a number of localities throughout the North Island (Thomas 1975; Berry 1990). Furthermore, various species from the genus *Trichogramma* have been used to control tortricid pests in many countries including China, France and parts of the United States of America (Russell 1987). Few species from the genus are known within New Zealand, one being *Trichogrammatoidea bactrae* and the other an unidentified species (J. Berry, pers. comm.). Host records within New Zealand have been observed from Lepidoptera, including the most common leafroller pests (Stevens 2000). The reported occurrence of parasitism on *S. macropetana* is therefore not unexpected. The degree to which egg parasitism is occurring by these species on *S. macropetana* remains unknown.

Even though predation was not observed in the current study, insect predators (as listed in section 4.3.2) were observed on leaves and within empty leaf rolls of

S. macropetana. The larval abundance of *Epiphyas postvittana* was believed correlated to predation by various arachnid species and an earwig species (*Forficula auricularia*) (Danthanarayana 1983). It is likely that predation by earwigs and other predators also impacts upon the abundance of *S. macropetana*, but this remains unquantified. Several more natural enemies of *S. macropetana* possibly exist, however in the current study their abundance was too low for them to be identified using the methods designed for the current study. One could conclude that other predators contribute little to the total mortality per generation and/or act in a delayed density dependent manner. It is widely accepted that natural enemies are important in the regulation of insect populations (Varley & Gradwell 1970). However, the regulation hypothesis has been challenged by Dempster (1983), due to the difficulty in detecting natural enemies as density dependent factors.

4.4.3 Limitations of sampling methodology

The accuracy of the current method was most likely limited by various factors, including the density of targeted development stages (i.e. difficulties of locating certain life stages at low densities); seasonal conditions effecting observed species and the observer (e.g. windy conditions created difficulties in observing shoot tips; rainfall forced adults into shelter and obscured egg location); and a lack of reproducible sites, as many of the eucalypt species were only represented once. The possibility of spatial differences of leaf rolls within a tree created a further limitation, as sampling from the ground may have over or under estimated the actual densities of leaf rolls present. Such limitations were restricted as much as possible, however, further improvements could be made by providing greater site reproducibility, and more systematic sampling.

5. Reproductive behaviour and preliminary identification of the female sex pheromone of *Strepsicrates macropetana*

5.1 Reproductive behaviour

5.1.1 Introduction

Biological information concerning a wide range of insect pests has proven invaluable for the development of insect pest management programs in the past (Apple & Smith 1976). As many lepidopteran species are key pests of valued commodities throughout the world, an understanding of insect reproduction is essential in developing successful management strategies. An increased understanding of insect reproductive behaviour has provided the basis of many pest management strategies in the past, including pest monitoring, pheromone trapping and mate disruption (Howse *et al.* 1998). This is the first quantified description of reproductive activity for *S. macropetana*, and will ultimately provide the biological knowledge required for pheromone extraction and identification.

5.1.2 Materials and methods

Forty male and 40 female pupae (< 3d old) obtained from the laboratory colony were weighed, measured and maintained at 20 ± 2°C, 60 - 70% RH. They were divided into two groups of equal size and sex ratio. The first group was maintained with a standard photoperiod of 16L: 8D h. Whereas, the second group was maintained with an inverse photoperiod of 8D: 16L h. Pupae were placed individually into transparent glass jars (6.5 cm height, 5 cm Ø), containing an egg sheet (paper towelling; 2 x 2 cm) and a food source (section 3. 2). Adult males (2-3d old) were paired with three to five day old females; this pairing was based on pre-mating periods from other tortricid species (Foster *et al.* 1995; Delise 1995). Scan sampling was performed on both groups for twelve hours a day, in which each pair was scanned every hour for 30 seconds and scored. Observations throughout the scotophase were conducted under a red light (Osram, 30W). The occurrence of various activities (e.g. inactivity, walking, flying, feeding, sexual activity and oviposition) was recorded until death. The data were corrected for the number of insects alive on each day, so that a frequency could be obtained for each moth. Graphical analysis of time and frequency data provided an understanding of the activity and sexual rhythm of *S. macropetana* on an hourly and daily basis. The total number of hatched eggs was used as a measure of egg viability.

5.1.3 Results

5.1.3.1 Description of reproductive behaviour

The reproductive behaviours of *S. macropetana* are described herein: Antennation typically occurred as a pre-copulatory behaviour but was occasionally observed after copulation. Wing fanning was observed only in adult males, in which the wings were rapidly fanned whilst standing towards the female. Mate calling was observed only in adult females. The antennae and abdomen were raised and the abdomen curved downwards, whilst the wings were elevated dorsally from the body and the ovipositor extruded. Pulsation of the abdomen and wings occurred at various times and frequencies throughout the scotophase. Copulation was exclusive to the scotophase, where the male and female were positioned back to back (180°), where they remained for approximately 40-120 min.

The oviposition behaviour of female *S. macropetana* consisted of three distinctive behavioural categories. Searching behaviour occurred as the female walked, whilst avoiding and repelling male contact ('mated-type' behaviour), in contrast with pre-copulatory activity ('virgin-type' behaviour). This activity occurred several times before the onset of egg laying. Whilst searching, the female reduced walking speed and extended wings above her body. The abdomen was curved at the tip and the ovipositor lobes (papillae anales) were extruded. Slow walking continued whilst the abdomen swayed from side to side probing the surface, and the antennae were kept in constant contact with the surface. Probing ultimately resulted in immobility, whilst the female fully protruded her ovipositor and pressed it against the chosen surface, on which egg laying commenced. This sequence was typically repeated several times throughout the scotophase.

5.1.3.1 Daily rhythm

The results indicated that *S. macropetana* is nocturnally active (Fig. 18), with physical activity occurring almost exclusively within the scotophase. However, walking, flying and sexual activity, were also evident within the first and final hours of the inactive period, i.e. the photophase. Sexual activity (e.g. male wing fanning, female mate calling and copulation) was most common during the first and second hours of the scotophase (Fig. 19). Female mate calling occurred in two distinctive peaks throughout the second and fifth hours of the scotophase (Fig. 19). These peaks were followed by a maximal response in male wing fanning at 4, 6, and 7 hrs into the scotophase. The second mate

calling peak resulted in a high frequency of copulation. Both calling and copulation continued into the initial hours of the photophase.

The methodology did not allow the recording of copulation times, but in many instances pairs were observed in copula in two subsequent observations (>1 hour). Pairs were not observed to copulate more than once. Oviposition behaviour was prominent around the second, fifth and seventh hours of the scotophase (Fig. 19) and continued into the first hour of the photophase. No direct relationship was evident between copulation and oviposition.

5.1.3.2 Lifetime rhythm

Strepsicrates macropetana appeared more active throughout days three to seven following emergence, with physical activity gradually declining thereafter (Fig. 20). All adults were given access to food prior to pairing, and a maximum feeding frequency was observed on the third day. Walking and sexual activity was prominent throughout the third to fifth day. Mate calling and copulation were evident immediately after pairing, with the number of calling attempts far exceeding the frequency of copulation. Both mate calling and copulation reached a maximum on the fourth day (second day after pairing), and gradually declined there after.

The search for oviposition sites gradually increased, peaking on days six and eight. Slightly more probing occurred than egg deposition, both reaching a maximum frequency on the seventh day (Fig. 20). The similarities of the probing and egg deposition curves indicate that these two activities are probably not mutually exclusive events. Furthermore, on days six and eight, searching behaviour far exceeded probing and egg deposition, indicating that the female did not accept every surface that was searched. Frequency of egg deposition increased, reaching a maximum on the seventh day, with a concurrent decline in inactivity and other behaviour. After which, inactivity increased, indicating adult activity levels were substantially influenced by insect age.

5.1.3.3 Total eggs laid and egg viability

Twenty females laid a total of 833 eggs, of which 629 (76%) were viable (Fig. 21). Over half (68%) the eggs were deposited on or before the seventh day after emergence. Egg viability declined with female age, with eggs laid on the eighth day having 55% viability, while only 31% viability was evident on the ninth day.

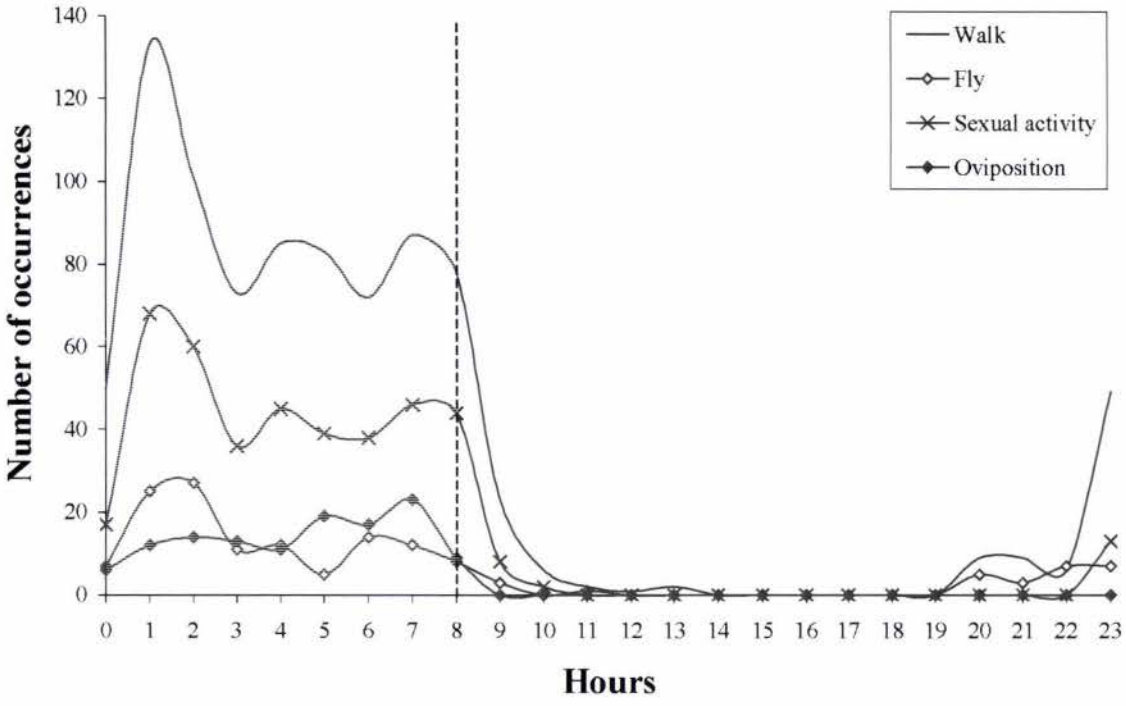

Fig. 17. Daily activity rhythm of *Strepsicrates macropetana*.
Hours 0 - 8 in scotophase (shaded grey); hours 8 - 0 in photophase (n = 80).

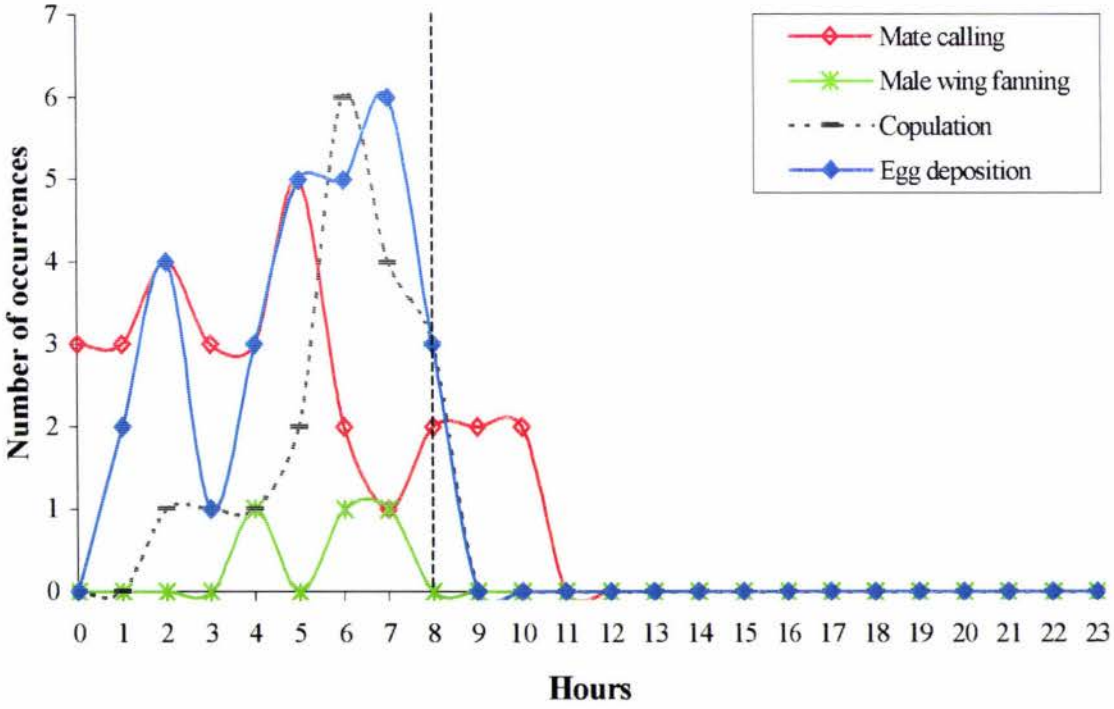

Fig. 18. Daily sexual rhythm of male and female *Strepsicrates macropetana*.
Hours 0–8 in scotophase (shaded grey): hours 9 – 0 in photophase (n = 80).

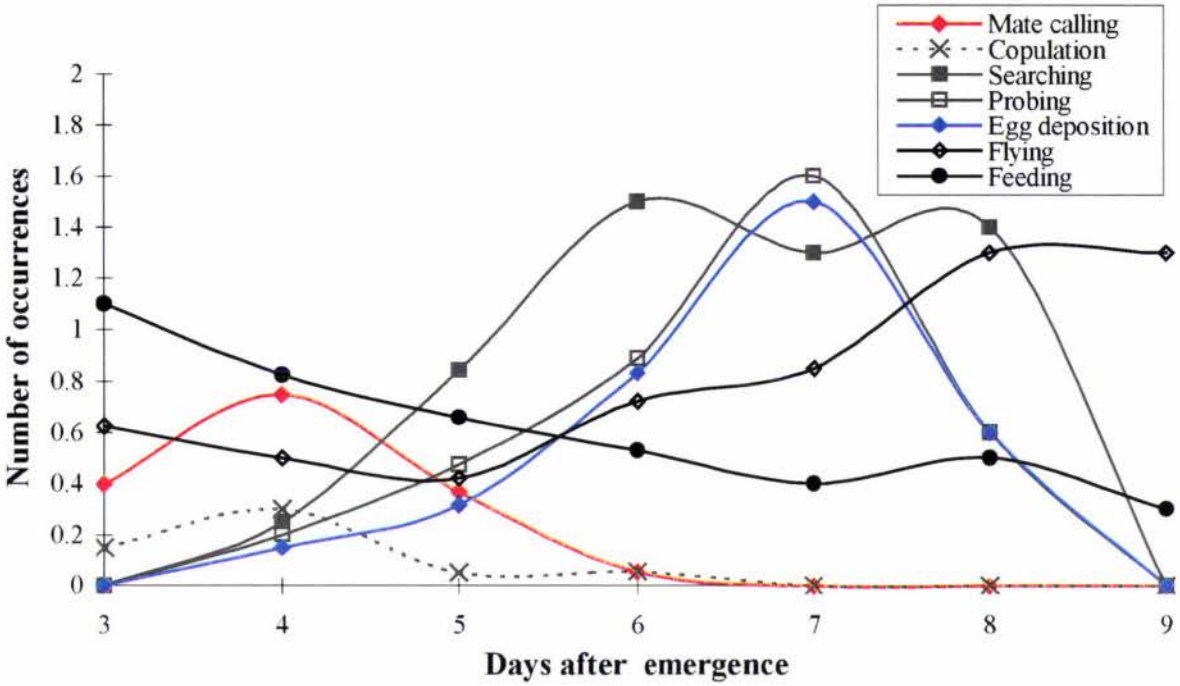

Fig. 19. Lifetime rhythm of *Strepsicrates macropetana* over a seven day period.

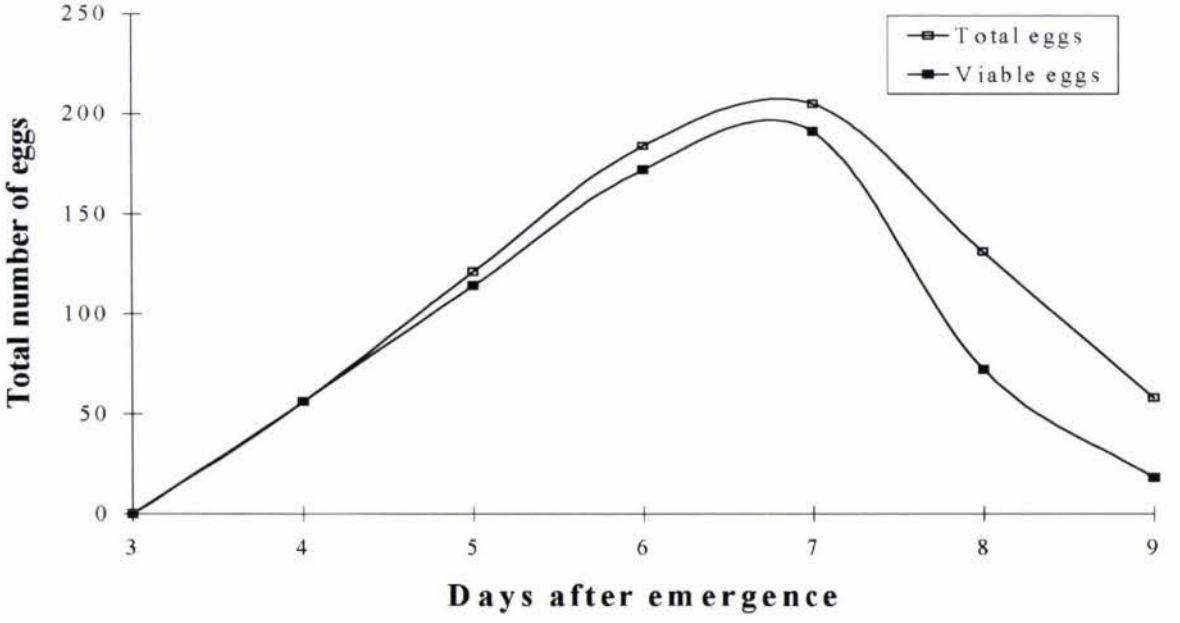

Fig. 20. The egg viability and total number of eggs laid by female *Strepsicrates macropetana* (n = 20).

5.1.4 Discussion

Each insect species has a unique pattern of reproductive behaviour that ultimately results in copulation and oviposition (Foster & Ayers 1996). The reproductive behaviour of *S. macropetana* is a relatively simple process, similar to other tortricids such as *Choristoneura fumiferana* (Clem.) (Sanders & Lucuik 1992). The daily reproductive rhythm of *S. macropetana* comprises four main steps. Firstly, any activity undertaken prior to mate calling was most common throughout the early hours of the scotophase (1hr). A peak in sexual behaviour was evident at this time, related to the increased interaction between male and female. The second step consisted of possible courtship behaviour, in which mate calling by the female (most common at two -five hours into scotophase) and male wing fanning (most common at four, six and seven hours into scotophase) occurred. It is likely that such activities resulted in the emission of volatile compounds to enhance mate attraction and acceptance. The third step consisted of copulatory activity. Copulation occurred predominately during the second half of the scotophase. Between the fifth and eighth hours, 83% of moths have been observed in copula, with only 17% copulation occurring throughout the first half of the scotophase. The occurrence of copulation was seemingly correlated with the prior occurrence of mate calling, indicating that female calling directed the timing of reproductive behaviour in *S. macropetana*. Furthermore, inferring that calling was an important orientation and location mechanism required for copulation.

Oviposition (searching, probing and egg deposition) was the final step of reproduction for *S. macropetana*. Oviposition did not directly follow copulation, therefore a period may be required for the spermatophore contents (sperm and nutrients) to move from the spermatheca to the vestibulum. It is commonly recognised that a variety of interacting chemical and physical stimuli are involved in the assessment of a host before egg laying occurs (Foster *et al.* 1997). The insect uses a variety of senses to assess the stimuli, for example, the mechano and chemosensory sensilla on the tarsi, antennae and ovipositor of most lepidopteran species enable the surface texture, chemistry and the appearance to be assessed (Foster & Howard 1998). Therefore, the searching and probing activities of *S. macropetana* possibly contribute stimuli utilised for such an assessment.

The reproductive rhythm of an insect is dependent on exogenous factors such as photoperiod and temperature (Baker & Cardé 1979). The copulation and mate calling of the tortricid *Cydia pomonella* is cued to photoperiod (Castrovillo & Cardé 1979). Reproductive rhythm also depends on endogenous factors such as hormonal control (Mbata & Ramaswamy 1990) and the age of the insect (Dunkelblum *et al.* 1987). Characters including calling periodicity, pheromone titre and release, mate responsiveness, copulation frequency, fecundity and fertility have been found to be age dependent in many lepidopteran species (McNeil 1991; Foster *et al.* 1995). Karalius and Büda (1995) found the reproductive success of *Ephesia kuehniella* Zl., *Cydia pomonella* and *Yponomeuta cognagellus* Hbn. to be greatly dependent on age. Furthermore, Delisle (1995) found that the mating success of the female tortricid, *Choristoneura rosaceana* (Harris) declined linearly with age. Similar age dependency was evident in the reproductive activities of *S. macropetana*. General and reproductive activities declined four to five days after emergence. The oviposition of *S. macropetana* reached a maximum frequency after seven days and declined thereafter. Furthermore, eggs laid seven or more days after adult emergence had a greater inviability.

Many lepidopteran species release volatile compounds throughout long and close-range courtship behaviour. Close range compounds are typically released by males from modified scent scales, which exist as either brush organs, hairpencils or tufts of hairs located on the insects abdomen, legs or wings (Horak 1991). The biological activity of such a compound has only been demonstrated for male *Grapholitha molesta* (Busck). This tortricid has an elaborate courtship display that involves the use of hairpencil organs to provide olfactory and anemo-tactile stimuli to attract the female at close range (Baker & Cardé 1979). Grant (1978) examined five tortricid species and found scent brushes and hair tufts within the costal fold of the forewing on all five species. As noted by Horak (1991), male tortricids possess a plethora of structures possibly utilised for the production and distribution of volatile substances. *Strepsicrates macropetana* males were observed rapidly wing fanning towards the vicinity of the female. It is likely that the male was emitting a close-range volatile compound to attract and orient the female for copulation. Male specific scales have been observed along the costal margin of the fore-wing on several *S. macropetana* males (J. Clearwater, pers. comm.).

5.2 Preliminary identification of the female sex pheromone of *Strepsicrates macropetana*

5.2.1 Introduction

Results from section 5.1 revealed that adult females performed characteristic abdominal pulsating during courtship. This behaviour has been associated with the release of a female sex pheromone in various tortricid species. For example, the female of *C. pomonella* curves her abdomen, extruding the ovipositor to expose the pheromone gland, whilst releasing a pheromone as a series of pulses, thus providing attractive stimuli for the male (Castrovillo & Cardé 1979; Howell 1991). Given this, the foremost objective of the current study was to examine whether males respond to females that pulsate their abdomen during courtship.

If a positive attraction of males towards females is obtained, an attempt will be made to collect, isolate and identify sex pheromone compound(s). Roelofs and Brown (1982) stated that the large majority of known tortricid pheromones predominately contain C_{12} and C_{14} acetates, with occasional C_{10} and C_{16} compounds present. Furthermore, pheromones within the subfamily Olethreutinae predominately contain C_{12} compounds (Horak *et al* 1988). Therefore, preliminary investigations aim to distinguish the major compound(s) of the female sex pheromone of *S. macropetana*.

5.2.2 Materials and methods

Pupae were obtained from the established laboratory colony (see Chapter three). Male (n = 300) and female (n = 300) pupae were placed in cages (30 x 30 x 30 cm), and the males were separated into a different bioassay room, thus limiting pheromone desensitisation. The conditions within the bioassay rooms were set at 18 ± 2°C; 60 - 70% RH, with a 16D: 8L photoperiod. Un-emerged pupae were removed at three-day intervals and placed into additional cages, enabling the approximate age of the adults to be monitored. The adults were fed as in section 3. 2. 1.

5.2.2.1 Attraction bioassay

A bioassay was performed to investigate the attraction of *S. macropetana* to conspecifics. Male (n=100) and female (n=100) adults were obtained from the above (section 6. 2). A metered air source was passed from a charcoal filter, to a humidifier, then into a glass 'Y' choice chamber (each arm 34 cm; 6 cm Ø) at 300ml/min (Fig. 22).

The ends of the chamber were blocked with metal mesh to prevent adults from escaping. The chamber was divided into three sections; release, treatment and control. Five treatment individuals were contained within a mesh box (6 x 6 x 6 cm) and placed within the treatment section of the Y- tube, these individuals were replaced after five replicates. One hundred replicates were performed for each treatment (Table 8). An identical mesh box (empty) was placed as a control in the other section of the Y-tube. To limit any positional effects, the control and treatment sections were rotated after five replicates.

Table 8. Treatments performed in the attraction bioassay.

	Treatment	Responder
1	Male	Female
2	Female	Male
3	Female	Female
4	Male	Male
5	Female extract	Male

Responding adults (n = 5) were collected from the original cage with an aspirator and placed into the release section of the chamber. Each replicate was terminated after ten minutes (stopwatch; DSE). After which the adults released were given either a positive rank if the moths were located between 0 and 4 cm from the treatment or control boxes or a negative rank if the moths were outside this predefined area. Responding adults were collected with an aspirator and transferred back to the cage of origin between each replicate. The apparatus was dismantled, washed with detergent and solvent, and baked at 200°C after every five replicates and between treatments. The bioassay was undertaken within the active part of the scotophase, predetermined in section 5.1.

Given the lack of normality, non-parametric tests were used for the analysis. A non-parametric Wilcoxon Rank Sum test was performed to examine the difference between the treatment and control groups. Furthermore, a non-parametric ANOVA (Kruskal-Wallis) was performed to detect any differences between the treatments.

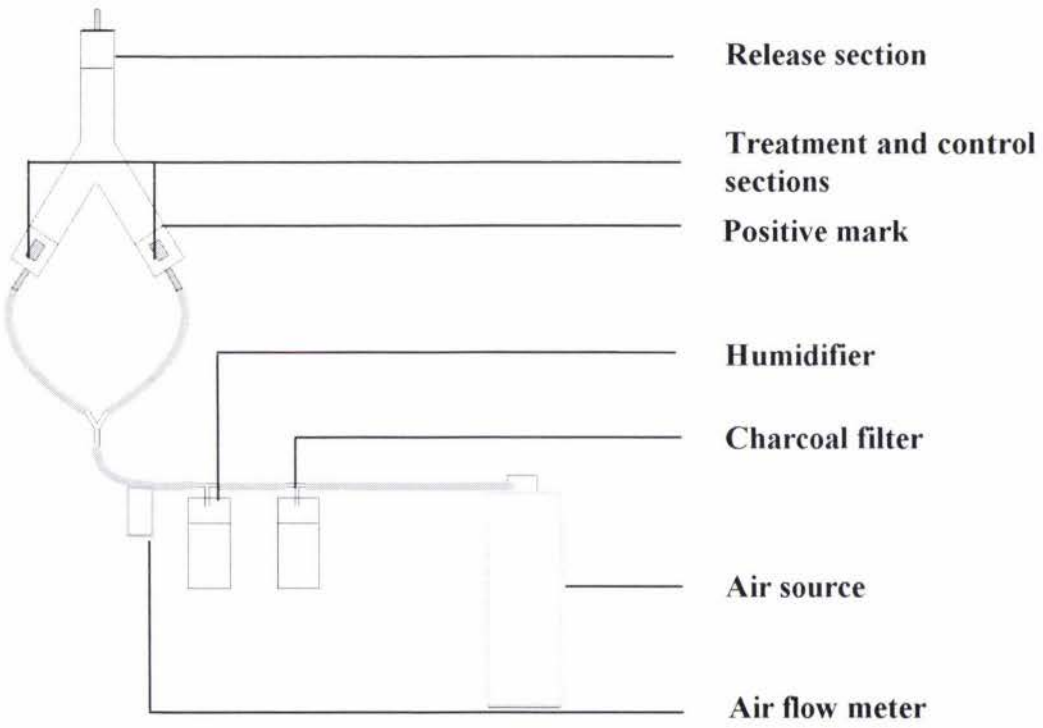

Fig. 21. Apparatus utilised for the attraction bioassay of *Strepsicrates macropetana*.

5.2.2.2 Collection, isolation and analysis of sex pheromone compounds

Tortricid pheromones have been identified with a variety of techniques in the past, with the determination of volatile retention times and identification of response profiles for an appropriate series of test chemicals being common procedure (Roelofs 1984). In the current study, the collection and analysis of volatile compounds of *S. macropetana* was attempted by effluvial collection (5.2.2.2.1) and gland extraction (5.2.2.2.2). Furthermore, the response of males to a variety of test chemicals was also investigated (5.2.2.4).

5.2.2.2.1 Collection of air-borne volatiles

Volatile collection was performed with the apparatus seen in Fig. 23, incorporating an enclosed airflow/filtration system. An air source was connected to a filtration system and was humidified before entering the glass chambers. The airflow system was metered at 180 ml/min into two vertically positioned glass chambers (36 cm length; 3 cm Ø), a control and an experimental chamber. Each chamber was two-piece, cylindrical in shape, and equipped with a charcoal filter and wire gauze for elevated mate calling points. A glass collection tube (115 mm length, 3 mm Ø) was connected to the top of each chamber, enabling the collection of any volatile compounds emitted. Each tube was packed with activated charcoal (untreated granular, 20-60 mesh; Sigma Chemical Company, USA) as an absorbing medium, with glass wool obstructing each end. Gas tight seals were maximised throughout the apparatus, with the use of silicon rubber seals, and Teflon and metal backed joints (Swaglok®). Contamination was minimised with the use of silicon tubing (i.d 1/4"; o.d 3/8"; wall 1/16": Cole-Palmer Instrument Company, USA) for connecting the apparatus. Once assembled, five to fifteen virgin female moths (depending on availability), between two to four days old, were transferred into the experimental chamber during the active part of the scotophase. The moths were left for up to four hours, during which wing pulsating occurred. On termination, the moths were collected with an aspirator and transferred back to the original cage. Collection was completed within the wind-tunnel room at Massey University, under a reverse light regime of 16D: 8L, a temperature of 18 ± 2°C, and 60 - 70% RH. After every replicate the apparatus was disassembled, washed (SC Johnson professional Emerald dishwashing liquid, Auckland, New Zealand), and rinsed thoroughly with distilled water and acetone, then left to dry. Subsequently, the temperature resistant apparatus was baked at 220°C for three hours, and then all apparatus were wrapped in aluminium foil for later use.

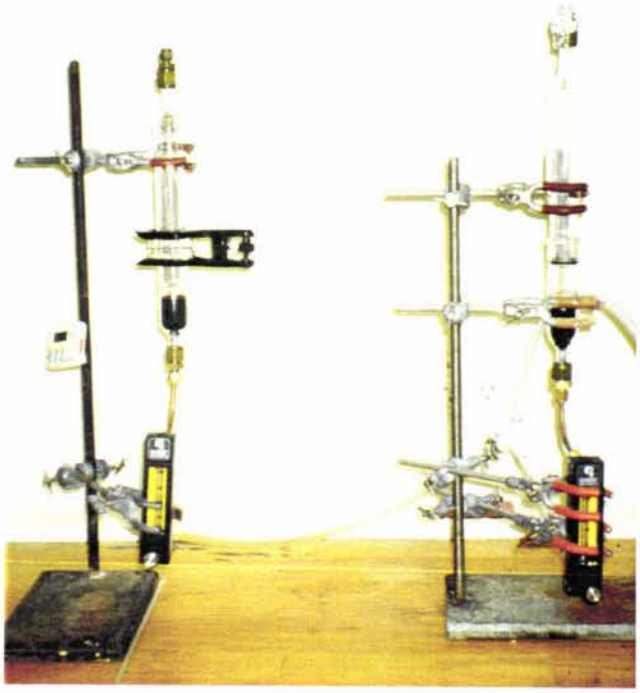

Fig. 22. Apparatus developed for the effluvial collection of *Strepsicrates macropetana*.

The collection tube was washed with 0.5 ml of distilled analytical grade *n*-pentane (HiPerSolv for HPLC™; BDH), and stored in a glass vial (2 ml; Sun International Frady Ltd) containing a glass conical (0.35ml), at -18°C until analysis. The sample was concentrated to 10 µl under a constant stream of nitrogen upon analysis. This process was repeated for every sample collected and each sampled was analysed as in section 5. 2. 2. 3.

5.2.2.2.2 Sex pheromone isolation using glandular extract

A classic method of pheromone collection within the tortricid family has been the extraction of the pheromone directly from the gland (Arn 1991). Between days two to four after emergence, virgin female moths were collected into scintillation vials (Wheaton, USA) and anaesthetized using carbon dioxide. The final two abdominal segments were extruded and excised, and the tissue surrounding the 8th and 9th abdominal segments was removed. All gland dissection took place using a Nikon dissecting microscope (10x/21eyepiece).

Dissected glands were placed into a glass conical (0.35 ml) containing 100µl of distilled analytical grade *n*-pentane, held with a glass vial (2 ml). Up to ten glands were present in each sample, but quantity was dependent on the availability of females. The glands were left to extract for approximately two hours before removal. The extract was then stored at -18°C until required for analysis. The samples were analysed as in section 5. 2. 2. 3.

5.2.2.3 Analysis of effluvial and glandular extract

A series of 12-monounsaturated acetate standards were sequenced to obtain maximum isomeric separation, giving basis for the program to be utilised for sample analysis (5. 2. 2. 2. 1 and 5. 2. 2. 2. 2). The analysis was performed using an HP6890 series gas chromatograph (GC) system. The GC was equipped with a flame ionisation detector (FID) and fitted with a DB-Wax column (30m x 0.32 mm i.d., phase thickness 0.5 mm; J & W Scientific). The injection mode was splitless for 60 seconds. Two temperature programs were utilised in the following experiment. The temperature for the first program was held at 60°C for three minutes, then increased to 155°C at 15°C/min, and from 155°C at 0.5°C/min until 168°C, therein increased by 25°C/min until 220°C. Throughout the second program, the temperature was also held at 60°C for three minutes, then increased to 155°C at 20°C/min, and increasing by 5°C/min until 159°C,

therein increasing by 0.1°C/min until 168°C, and finally increasing by 25°C/min until 220°C. The injector temperature was set at 250°C and the detector at 275°C. The carrier and make-up gases were hydrogen and nitrogen, respectively. Each sample (1µl) was injected into the capillary column with a syringe (10 µl; Hewlett Packard) cleaned thoroughly with solvent. The area and retention times obtained for the 12-monounsaturated acetate standards were compared to those acquired for the samples, making it possible to identify the components tentatively by comparison.

The antennal response of males to female effluvial and glandular extract was investigated using a coupled gas chromatograph electroantennogram (GC-EAD) system. The effluent from the GC capillary column was delivered simultaneously to the antennal preparation and the GC detector via a glass Y-splitter. The biological significance of the sample was gauged in relation to the retention time of the compounds present and the subsequent response of the male antennae to the sample (see section 5.2.2.4). Results are graphically presented.

5.2.2.4 Electroantennogram assay

The specificity and sensitivity of the male's antenna to various compounds makes it an effective means for assaying pheromone components and predicting the general nature of the pheromone (Roelofs 1984). An electroantennogram (EAG) assay was performed using antennae freshly excised from ten adult males (n = 20 antennae), from which each antenna was used once. Males were anaesthetized with carbon dioxide and the antennae subsequently excised at the basal segment. The tip segments of the antennae were also excised, ensuring an electrical flow through the connection. Individual antennae were suspended between two electrodes with an electrode gel (Spectra®360; Parker Laboratories, Inc, USA), providing adhesion to the ends of the silver wire. Each electrode was covered with a glass pipette, which prolonged the life of the antennal preparation and minimised outside electrical interference. Each antennal preparation occurred under a dissecting microscope (10 x 21 eyepiece). Electrical responses from the antenna were passed through an amplifier, with subsequent processing performed by means of a PC-based interface and EAG software (Syntech, Hilversum, The Netherlands).

Based on pheromonal evidence from closely related species, the antennal response was examined against an appropriate series of standards from the 12 and 14 monounsaturated acetate series, including all positional isomers (*E Z*) (HortResearch, Auckland). Isomers (10 µg) were absorbed onto labelled pieces of filter paper and inserted separately into glass Pasteur pipettes (150 mm; Volac). To elicit an EAG response, a pulsed humidified air current was driven through the pipette and directed onto the antennal preparation. Sources were chosen at random from the series, with a different combination repeated every time, equated to a total of 20 replicates for each isomer. A reference compound (12:Ac) was applied regularly to the preparation to monitor for desensitisation. Antennal responses were normalised to correct for any decline in reference response by linear interpolation. The relative response recorded for each replication was recorded graphically and summed overall to give a sample average and deviations about the average. An ANOVA with a Duncan multiple comparative test was performed to detect any difference in antennal response between the positional isomers of the 12:Ac series.

5.2.3 Results

5.2.3.1 Attraction bioassay

The degree of response towards the treatment was typically high when the treatment was female and the responder a male (Fig. 24), substantiating the possibility of an attractive stimulus between the treatment and responder individuals. In addition, the degree of response by the responder was consistently low towards the treatment when males were utilised and towards the control box. This indicated that such were not attractive to other individuals. A significant difference was obtained between the different treatments ($U = 104.16$; $df = 4$; $P < 0.0001$). Thus varying degrees of attraction existed between the treatments, with male-to-male replicates showing the least attraction, and a highly significant response shown when the female extract and female were used as a treatment (Fig. 25).

5.2.3.2 Collection, isolation and analysis of sex pheromone compounds

Samples containing air-borne volatiles did not reveal any peaks within the chromatographic profile, therefore indicating a lack of detectable biologically active compounds within the sample. The samples were consequently discarded. In contrast, consistent chromatographic peaks were obtained in a number of samples containing the glandular extract. A typical result is shown in Fig. 26, where two main peaks were

evident. With the use of the GC temperature program two for sample analysis, retention times were observed at 12.392 and 13.265 minutes. After comparison with the standard compound (12- carbon acetate), it was evident that the first peak within the sample was consistent with the retention time of *E*7-12:Ac. The second peak was observed at a retention time the same as *Z*8-12:Ac within the standard (analysed with temperature program 1).

A strong antennal response was evident at a retention time of 12.35 minutes using the GC-EAD procedure (Fig. 27). This was followed by a smaller antennal response at 13.27 minutes. These antennal responses corresponded with small GC peaks, indicating the presence of biologically responsive compounds within the sample. After close observation and comparison with the standard and preliminary GC results, it was evident that the peaks corresponded to the retention times of *E*7-12:Ac and *Z*8-12:Ac. Therefore, based on the evidence from GC and GC-EAD analysis, it was tentatively concluded that the female sex pheromone of *S. macropetana* contains a mixture of (*E*)-7-Dodecenyl and (*Z*)-8-Dodecenyl acetates. However, as this was only preliminary analysis, it does not preclude the existence of other compounds.

5.2.3.3 Electroantennogram assay

The main biologically active compound was within the 12-carbon acetate series, providing a greater overall EAG response than the 14-carbon acetate series (3.6 ± 0.3; 2.1 ± 0.3 mV, respectively). A significant difference in amplitude was found between the various isomers of the 12-carbon acetate series ($F = 2.44$; $df = 17, 18$; $P > 0.03$). The greatest relative and average amplitudes were achieved at *E*7-12:Ac, which was slightly greater than the response at *Z*7-12:Ac (Figs. 28 & 29). No significant difference was detected between the two isomers. Given the lack of statistical separation, the major component of the female sex pheromone is likely to be one of the following compounds, *E*7-12:Ac or *Z*7-12:Ac. Based on the EAG results, minor components of the pheromone may also include *Z*5-12:Ac, *E*6-12:Ac and *Z*6-12:Ac. However, the response of the males may be minimal to minor components in isolation.

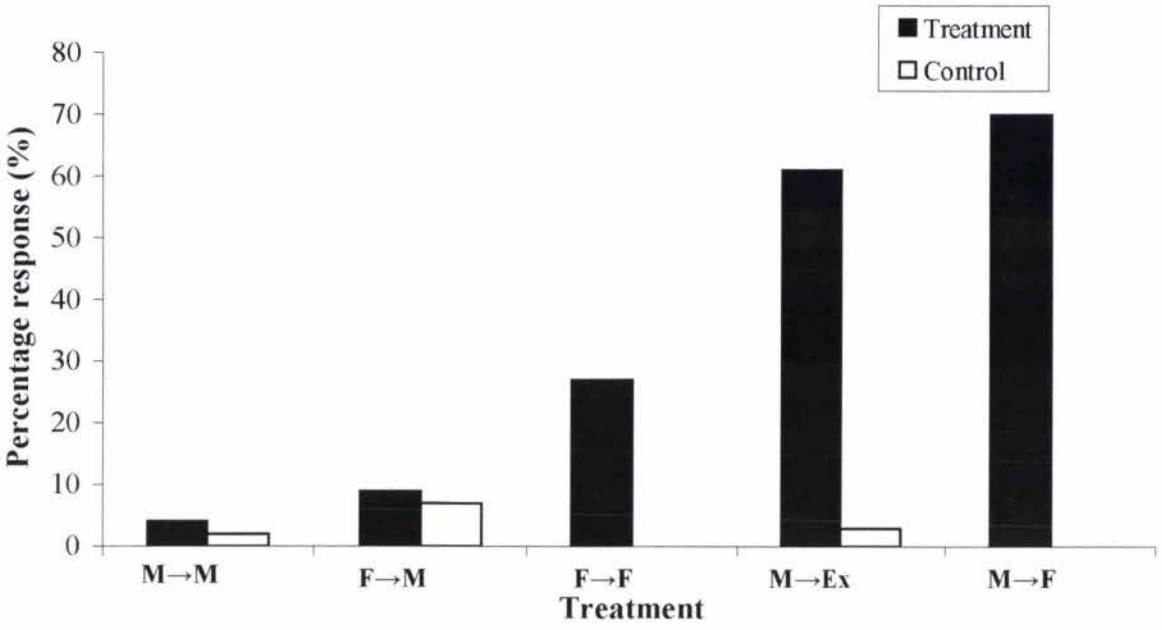

Fig. 23. Response of *Strepsicrates macropetana* to treatment and control stimuli (M, male; F, female; Ex, female extract; → response to).

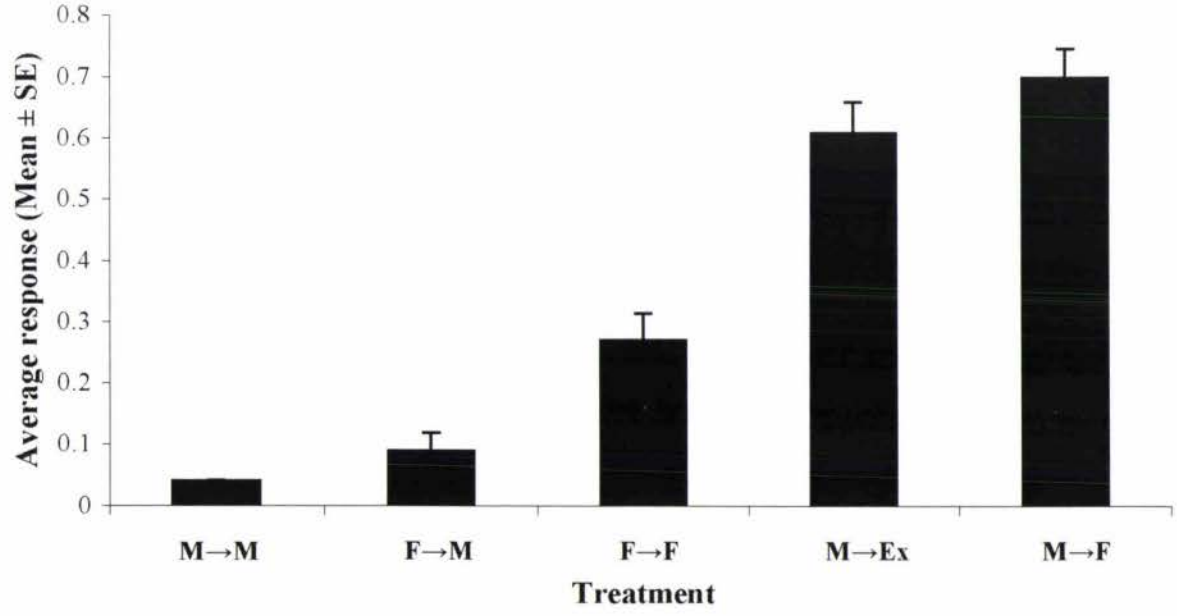

Fig. 24. Response of *Strepsicrates macropetana* to various treatment stimuli (M, male; F, female; Ex, female extract; → response to).

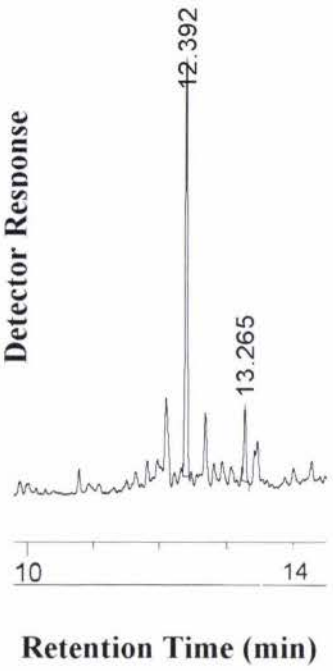

Fig. 25. Gas chromatograph of the glandular content extracted from female *Strepsicrates macropetana* (n = 7). Analysed using temperature program 2.

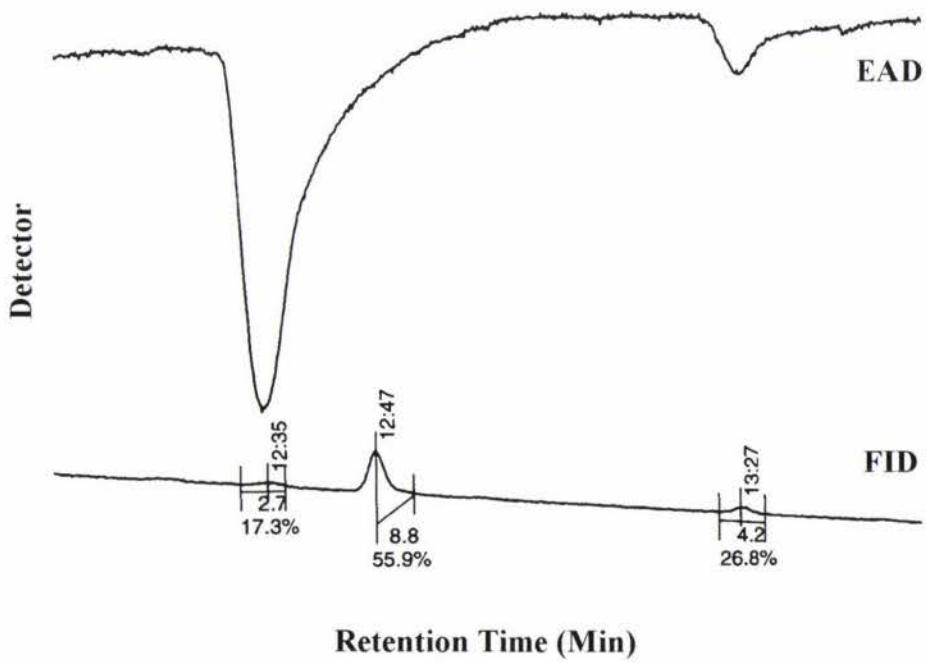

Fig. 26. Antennal response to glandular extract of female *Strepsicrates macropetana* during GC-EAD analysis. Analysed using temperature program 2.

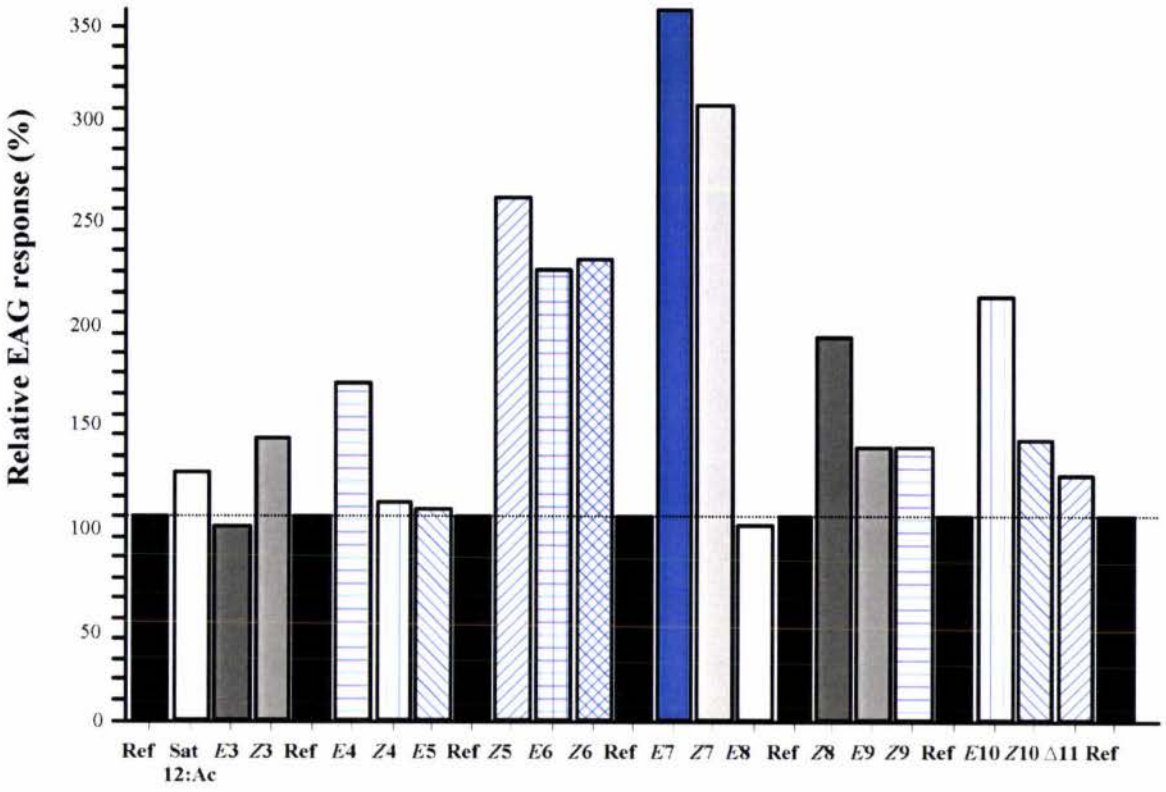

Fig. 27. The typical EAG profile of a single male antenna of *Strepsicrates macropetana* to a series of positional isomers within the 12:Ac group (data has been normalised; black bars represent reference compound).

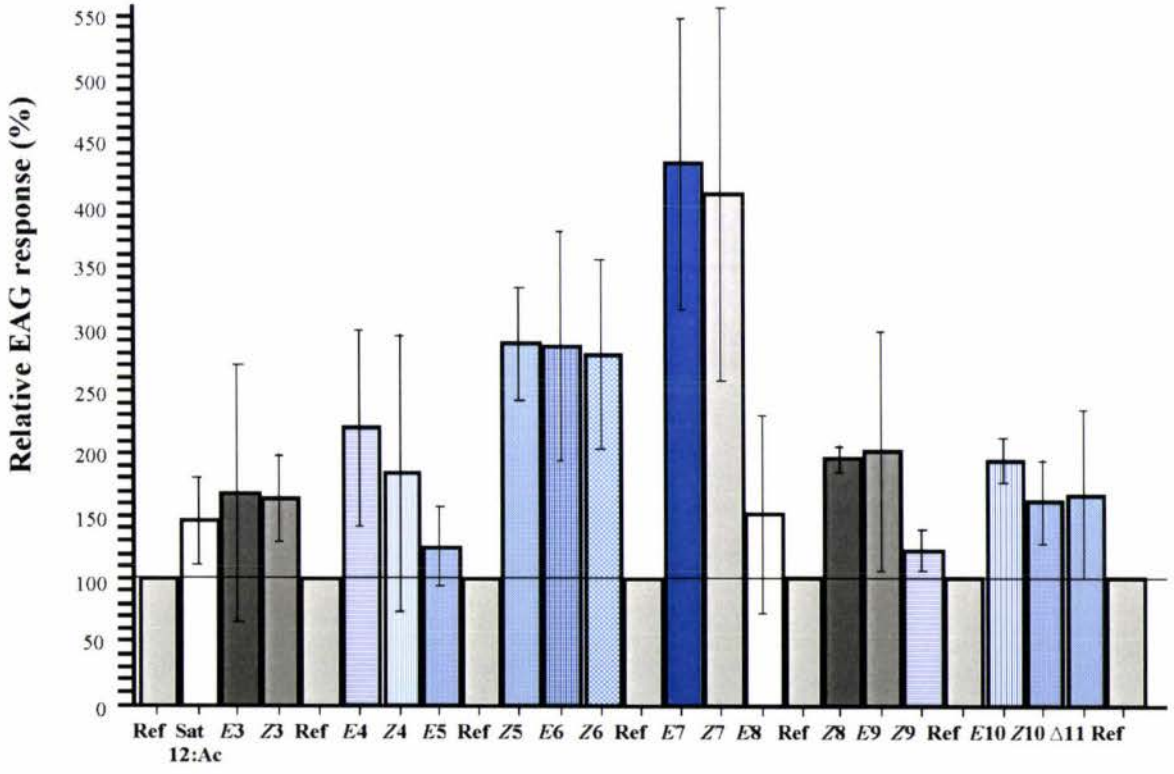

Fig. 28. The average EAG response of male *Strepsicrates macropetana* to a series of positional isomers within the 12:Ac series (n = 20 antennae) (data has been normalised; grey bars represent reference compound).

5.2.4 Discussion

The attraction that males experienced towards the control stimuli was limited. Based on evidence provided in this chapter, it is clear that the presence of chemical cues from the female provides attractive stimuli for adult males of *S. macropetana.* It would also appear that other stimuli, such as visual and/or tactile, played a role in short distance mate attraction, as the female treatment alone achieved the greater level of male response in comparison to the extract. As stated by Baker (1989) "we are only beginning to appreciate the complexities of the integration of chemical and visual stimuli they (male moths) perform in the process" (cited in Foster & Harris 1992b). However, it may also be possible that the extract had a different composition to that emitted by the female.

The main biologically active component(s) found by EAG and GC-EAD, was evident within the 12-carbon acetate series, which gave a greater response than the other carbon acetate series tested. The *E*7 and *Z*7 positional isomers produced a greater response than did any other from the same series. The major component of the female sex pheromone of *S. macropetana* was subsequently revealed as (*E*)-7-Dodecenyl acetate. Other components, in particular *Z*8-12:Ac, *Z*7-12:Ac, and to a lesser extent *E*6-12:Ac, *Z*6-12:Ac and *Z*5-12:Ac indicated moderate responses through EAG and GC-EAD analysis. However, minor components in isolation from the rest of the pheromone blend have been known to give a fairly weak antennal response by comparison, such synergistic properties have been reported for many other species (e.g. Bellas *et al.* 1983; Tamaki 1977; Hewlett 1969).

The sex pheromones previously identified within the tortricid family typically comprise primary alcohols, their corresponding acetates and aldehydes. (*E*)-7-Dodecenyl acetate has been identified as a relatively common sex pheromone component within this family (The Pherolist 2000). Within the subfamily Olethreutinae, both *Ancylis sativa* Lui. and *Grapholita endrosias* Meyrick contain this component within their identified sex pheromone blend. This component has also been reported from other lepidopteran families, including Gelechiidae and Noctuidae. The components (*Z*)-7-Dodecenyl and (*Z*)-8-Dodecenyl acetates have been identified from several species within the tortricid family and tribe Eucosmini; examples include *Eucosma womonana* Kearfott, and *Spilonota ocellana* Denis and Schiffermüller, respectively (The Pherolist 2000). These components have also been identified from

sex pheromones within many other lepidopteran families, including Oecophoridae, Xyloryctidae, Coleophoridae, Cosmopterigidae, Gelechiidae, Plutellidae, Zygaenidae, Pterophoridae, Pyralidae, Geometridae, and Noctuidae (The Pherolist 2000). Based on such evidence it is no surprise to find these as components within the sex pheromone of *S. macropetana.*

The procedures used for purification, analysis and identification of biologically active compounds often depend on the nature of the pheromone to be identified, but in situations where the compounds are unknown various methods often need to be employed (Hummel & Miller 1984). The methods and apparatus utilised in the current study provided high-resolution gas chromatography for resolving the isomers of monounsaturated compounds typically found in the pheromone blends of lepidopterans, and fulfilled the required sensitivity to detect minute traces of the compounds present. The collection of *S. macropetana* effluvia was unsuccessful, as no biologically active compound was detected within the numerous samples analysed. In addition, no difference was found between the sample and control traces. The environmental conditions within the glass chamber, such as the glass surface, the air pressure, and the number of moths present, could have contributed to an unsuitable environment for mate calling, i.e. pheromone release. Furthermore, due to minute quantities of volatiles typically emitted by females, the collection apparatus may have been an inappropriate medium of collection.

The predominance of glandular extraction as a method for identifying leafroller pheromones has been noted in the literature (e.g. Hill & Roelofs 1979; Bellas *et al.* 1983; Foster & Roelofs 1987; Foster *et al.* 1990). However, it has been demonstrated by various authors (Arn 1991; Hill *et al.* 1975) that the constituents and the ratio of components within an insect sex pheromone gland is often different from the volatile compounds emitted by the female. For example, the pheromone gland of *Spilonota ocellana* (Denis and Schiffermüller) was found to contain *Z*8-14:Ac, *Z*8-14OH and 12:Ac. When the effluvia of this species was collected and analysed it was found to contain the same compounds but in different proportions (The Pherolist 2000). Nevertheless, male antennae of *S. macropetana* were still responsive to glandular extract supporting the results from the behavioural study.

Overall, the current study has demonstrated the nature of the female sex pheromone for *S. macropetana*. For this information to be utilised in a pest specific management program, subsequent research is required to confirm the attractiveness of a synthetic blend on the natural population. Many tortricid pests within New Zealand have been successfully monitored with the aid of synthetic pheromones (see section 2.2). Such a method would prove useful in the management of *S. macropetana* if used in conjunction with toxic bait or in the regulation of other management strategies to be employed.

6. Concluding Remarks

The current research revealed an extensive amount of information regarding the biology and ecology of the eucalypt pest, *S. macropetana.* In the laboratory, use of eucalypt foliage as a food source for rearing of *S. macropetana* resulted in a shorter development time, heavier pupal weights, a higher survival rate and greater fertility in the current study, compared to those reared on artificial diet (GPD). Future research could investigate the development of a more nutritionally compatible artificial diet for the rearing of *S. macropetana*. Even though a feasible rearing method was developed in the current study, the development of an artificial diet would eliminate the need for such a large cage for rearing on potted host plants. Additionally, as the greatest mortality occurred throughout the larval period, irrespective of diet, it would be best to optimise larval development to improve colony success.

It was found that *S. macropetana* developed through five larval instars that were not discernable by their head capsule widths alone, therefore, future identification of larval instar can be aided by the apparent morphological differences. Sexual dimorphism was present in the late instar larva, pupa and adults, including heavier female pupal weights, the number of movable abdominal segments present on the pupa, positioning of the anus and genital openings, adult colouration and antennal morphology. *Eucalyptus nitens* and *E. regnans* were concluded to be the better species for larval development, giving greater pupal weights, shorter development time and the greatest fecundity. Given a choice between eucalypt, non host (apple) foliage and other surfaces within the test arena, females laid significantly more eggs on the eucalypt foliage. Furthermore, *S. macropetana* showed a preference for ovipositing on the lower surface of the leaf in some of the species examined. *Strepsicrates macropetana* laid the greatest proportion of eggs on the central-mid vein region with very few eggs laid between the veins on the leaf surface. In other studies oviposition behaviour of this type has been attributed a preference for a rougher substrate texture for egg laying. The selection of a host plant for oviposition may be important in host selection for reasons unrelated to larval growth and survival, such as to encourage dispersal or to decrease competition (Foster & Howard 1999).

Observation from field populations of *S. macropetana* indicated that younger larvae preferred to feed within established leaf rolls, and in shoot tips and buds,

whereas, older larvae were also found on older foliage. *Strepsicrates macropetana* was observed to develop through four to five generations per year corresponding to season, with a possibility of overlapping generations occurring throughout the summer season due to shorter generation times. Temperature and the eucalypt species used for development had a significant influence on the abundance of *S. macropetana,* whereas the site had little effect. *Strepsicrates macropetana* was most common to *E. microcorys, E. fastigata, E. brookerana* and *E. nitens*. This has been attributed to various ecological, physiological and/or chemical differences in the host plant between season, site and species. The pupal weight of field developed *S. macropetana* was influenced by the eucalypt species developed on, site and temperature. The predominant natural enemy found in sites examined throughout the Manawatu and Bay of Plenty regions was *Trigonospila brevifacies*, with larval parasitism observed up to 45%. Three peaks in parasitism were observed subsequent to a decline in *S. macropetana* abundance. This tachinid has been recognised as a common parasitoid of other leafroller pests present in New Zealand orchards, including *Ctenopseustis obliquana*, *Epiphyas postvittana* and *Cnephasia jactatana*. Many questions still remain about the phenology, abundance and natural enemies of *S. macropetana.* It was been stated by Solomon (1991) that the study of a forest insect pest typically requires a long-term effort by a large team of biologists and even biometricians. Therefore, the current study provides the foundation for more in depth research.

Strepsicrates macropetana was determined to be nocturnally active with sexual and ovipositional behaviour predominant within the scotophase. It was found that *S. macropetana* became sexually active after three days, behavioural activities included female male calling, display or wing fanning by the male, and copulation. This sexual behaviour gradually subsided after adult moths were five days old. Oviposition activities peaked on the sixth and eighth day after emergence, and were most common around the second, fifth and seventh hours of the scotophase. Oviposition behaviour included searching, probing and egg deposition. The reproductive activities displayed are typical of the reproductive activities of many tortricid species, however some species appear to have a more complex routine incorporating intricate displays (Baker & Cardé 1979). Overall, sexual activity was most common during the first and second hours of the scotophase, in which mate calling was most frequent throughout the second and fifth hours. The description of sexual activity and the determination of the female mate calling period enabled the appropriate time to be determined for sex

pheromone collection. Many questions remain about the host finding and reproductive behaviour of *S. macropetana*.

The current study confirmed an attraction of adult males towards females, therefore, a method was pursued to collect, isolate and attempt to identify the components involved in such attraction. Based on the results obtained from GC, GC-EAD, and EAG analysis, the major pheromonal component evident was (*E*)-7-Dodecenyl acetate. Other components, in particular *Z*8-12:Ac and *Z*7-12:Ac were also indicated as biologically active through EAG and GC-EAD responses. The correct blend of pheromone components needs to be identified in the laboratory then confirmed in the field during future research. The correctly identified sex pheromone could then be used for practical application in a pest management program.

The current research provides a basis for future research with *S. macropetana.* Although the findings of the current study may not provide direct applications for the purpose of *S. macropetana* management in the field, it does provide basic information on the biology and ecology of *S. macropetana* that will be useful in further research on this pest of eucalypts in New Zealand. Possible management options for *S. macropetana* could include systematic spraying timed to peak larval infestation levels, parasitoid introductions, sex pheromone trapping and mate disruption. Many of which have been successful in other leafrollers in New Zealand (Tomkins *et al.* 1991b; Wearing 1979; Wearing *et al.* 1991).

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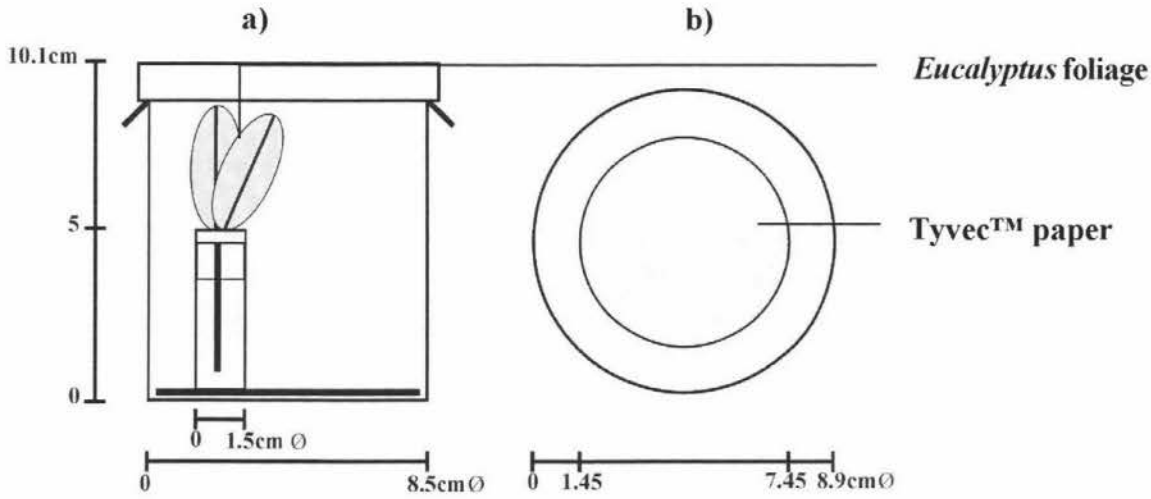
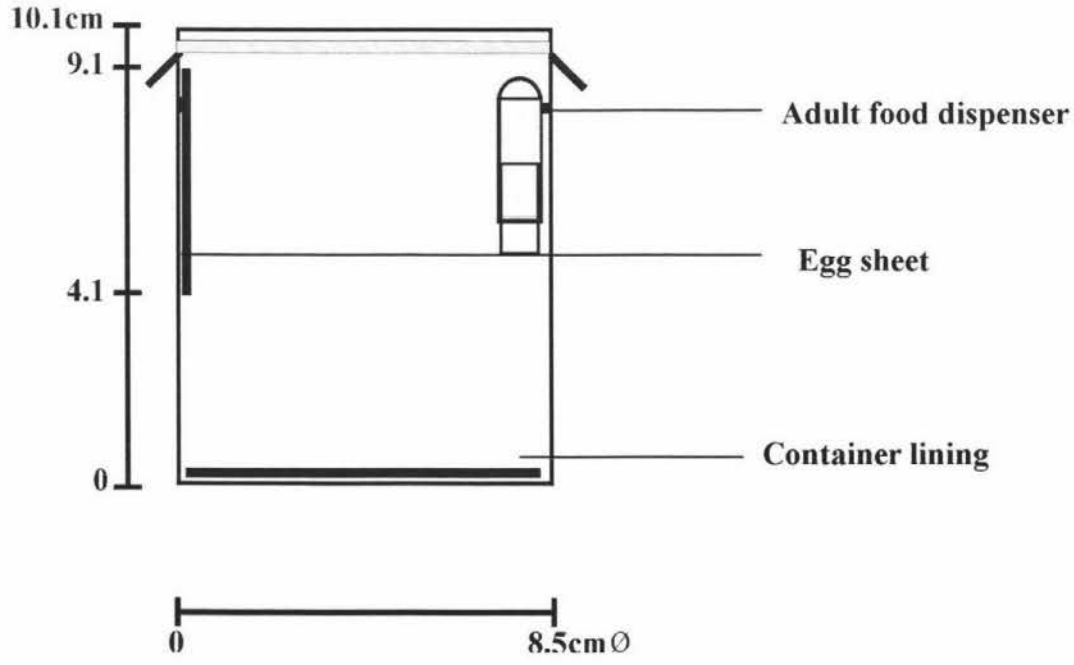
Appendices

Appendix one:



Apparatus utilised for developing individual *Strepsicrates macropetana* on *Eucalyptus* foliage; a) side view of the rearing container; b) top view of lid showing the incorporation of Tyvec™ paper into the lid for ventilation.



The container utilised for the mating and oviposition of adult *Strepsicrates macropetana*.

Appendix two:

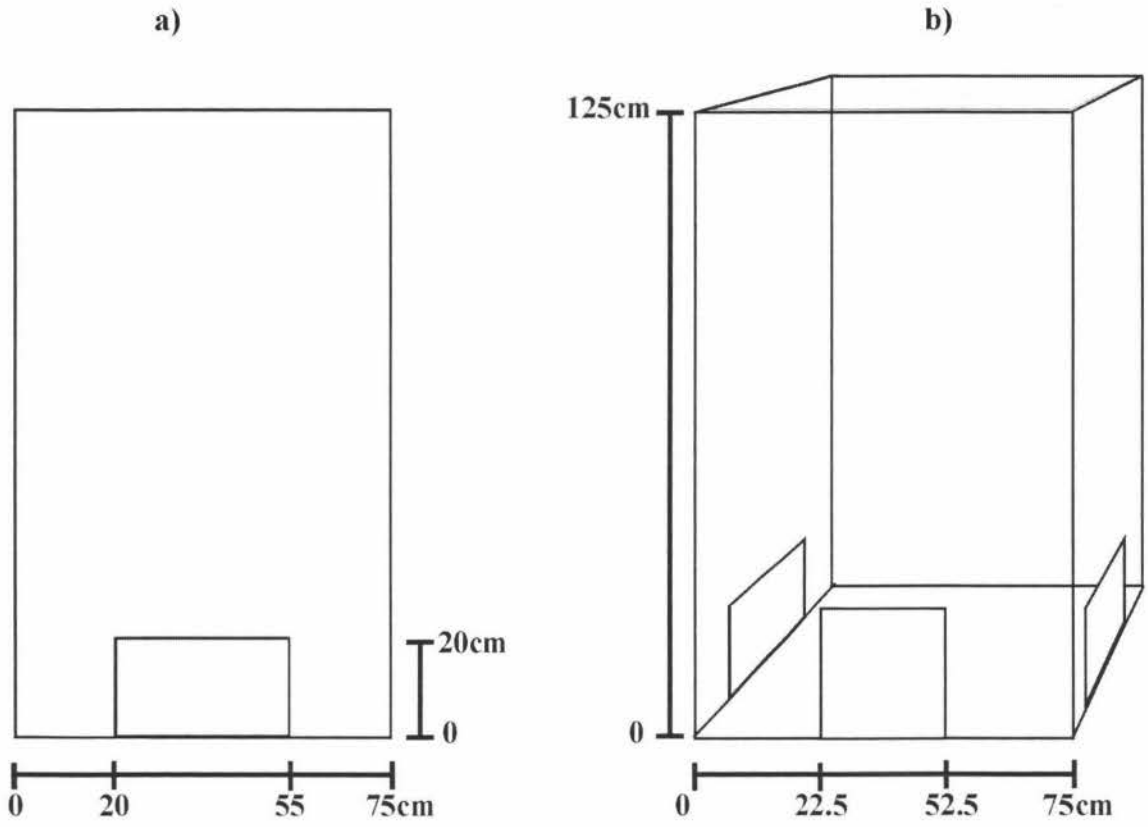
Below is the recipe for the general-purpose diet (GPD) utilised to rear *Strepsicrates macropetana:*

GPD 3kg	
INGREDIENT	AMOUNT
Dry Mix	610g
Cholesterol	1.5g
Water	2160ml
Linoleic Acid	7.5ml
Vanderzant	60g
Sucrose	90g
Glucose	15g
Streptomycin	450mg
Penicillin	450mg
Water	300ml
Mould Inhibitor	45ml
Prochloraz	120mg

MOULD INHIBITOR 4L	
INGREDIENT	AMOUNT
Nipagin	300g
Sorbic Acid	400g
95% EtOH	3400ml

DRY MIX FOR 72kg	
INGREDIENT	AMOUNT
Cellulose Powder	7200g
Casein	2520g
Agar	1800g
Wesson's Salt Mix	720g
Wheatgerm (Fine)	2160g

Appendix three:



Cage developed for mass rearing *Strepsicrates macropetana* with potted *Eucalyptus* foliage; a) side view showing the mesh vents; b) three-dimensional view.

Appendix four:

Climatical data obtained from NIWA stations located at Whakatane (B76996) and Grasslands, AgResearch, Palmerston North (E05363).

NUMBER	YYYY	MM	RRR	RRD	RWD	RMX	TME	TMX	TMN	EMX	EMN	RHP	SUN
E05363	1999	1	39.4	10	8	11.2	19.9	25	14.9	28.7	8.6	78.2	256.6
B76996	1999	1	96.1	9	8	50	21.3	25.5	17	28.8	10.6	74.6	238.6
E05363	1999	2	20.1	3	1	19	19	24.9	13.1	28.8	5	72	242.4
B76996	1999	2	17.9	3	3	13	19.4	24.2	14.5	26.2	9.3	72.4	235.3
E05363	1999	3	34.3	10	6	7.2	19.1	23.9	14.3	28.4	11.5	79.6	193.3
B76996	1999	3	75.6	13	10	27.5	20.1	24.3	15.9	26.5	11	82.9	176.1
E05363	1999	4	65.3	9	8	29.1	14.7	19.3	10.1	25.5	2.4	76.5	174.9
B76996	1999	4	62.5	10	8	14.5	16	21	11	24.6	2.7	81.1	169.4
E05363	1999	5	114.6	13	12	31.3	12.2	16.9	7.6	21.1	1.4	89.6	102.3
B76996	1999	5	97.2	11	9	59.3	13.9	18.8	9.1	21	3.4	86.3	140.9
E05363	1999	6	67.9	14	10	17.2	9.5	14.2	4.9	17.4	-1.1	89.7	118.8
B76996	1999	6	126	10	10	34	11.2	16.2	6.2	19.7	0.2	89.9	143.7
E05363	1999	7	94.5	21	14	18.5	9.2	13.5	4.9	19.2	-3.1	86.3	102.1
B76996	1999	7	141.5	10	8	47	10.2	15.5	4.8	18.5	0	88.5	161.4
E05363	1999	8	86.5	16	13	15.3	8.4	13.4	3.4	17.2	-1.4	88.1	139.6
B76996	1999	8	147.4	12	10	38.5	10.3	15.9	4.7	20.2	-0.5	83.1	194.4
E05363	1999	9	49.6	12	7	14.1	11	15.8	6.1	19.3	-2.3	81.1	157.3
B76996	1999	9	152.7	12	10	62.5	12.8	18	7.5	23	1.3	77.6	194.3
E05363	1999	10	34.9	15	7	12.2	13.8	18.4	9.2	23.2	1.2	88.4	157.1
B76996	1999	10	91.4	8	8	60	14.9	19.4	10.5	24	3.9	79.6	221.9
E05363	1999	11	125.9	15	13	23.9	15.1	19.5	10.7	24.7	1.4	83.8	132.3
B76996	1999	11	222.2	17	15	70	16.9	20.5	13.2	22.5	6.3	79.6	174.1
E05363	1999	12	66.4	12	8	29.6	15.3	19.8	10.9	23.4	3.1	85.2	160.1
B76996	1999	12	68.2	9	7	16.5	17.6	22.1	13.1	26	6.3	72.7	222.1
E05363	2000	1	125.1	10	8	48.3	17.3	22.2	12.5	30.4	6.8	83.1	210.6
B76996	2000	1	74.9	14	12	22.5	19	23.1	14.9	25	9.8	78.7	205.7

Key for above data:

RRR - monthly rainfall total in millimetres
RRD - number of days with rain =>0.1mm
RWD - number of days with rain =>1.0mm
RMX - highest 1 day total
TME - mean daily temperature in degrees Celsius
TMX - mean daily maximum temperature
TMN - mean daily minimum temperature
EMX - extreme (highest) maximum temperature
EMN - extreme (lowest) minimum temperature
RHP - mean relative humidity percentage
SUN - monthly total of bright sunshine hours

Appendix five:

Life history and abundance of the *Eucalyptus* leafroller, *Strepsicrates macropetana* (Lepidoptera: Tortricidae). Proceedings of the 52nd New Zealand Plant Protection Conference, 108-112.

LIFE HISTORY AND ABUNDANCE OF THE EUCALYPTUS LEAFROLLER (*STREPSICRATES MACROPETANA*)

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ABSTRACT

The Eucalyptus leafroller, *Strepsicrates macropetana* Meyrick, has become a pest of increasing economic importance to young eucalypt plantations in New Zealand. Damage to shoot tips, leaves, and developing flowers can potentially impact on tree form and growth. Neither *S. macropetana* life history nor abundance in the field has been well researched up until now. A laboratory study showed that larvae developed through five instars, with colour ranging from translucent green/yellow to a pink/red. A full life cycle of this species was completed within 46.2 ± 11.4 days (mean ± SD) under laboratory conditions (20°C ± 2°C) on *Eucalyptus macarthurii*. A survey over 1998/1999 summer within the Manawatu region indicated that average leafroller occurrence was greater than five active individuals per tree on five of the fifteen *Eucalyptus* species examined. Of those five species, abundance was greater on trees without adult foliage. This insect occurred predominately within webbing about the apical shoot tips, and although rare (0.89%), up to six larvae were sometimes present within the same webbing. More detailed investigations, including the number of generations occurring per year in the field, is currently being carried out.

Keywords: Tortricidae, *Strepsicrates macropetana*, leafroller, *Eucalyptus*, life-history, abundance.

INTRODUCTION

The *Eucalyptus* leafroller, *Strepsicrates macropetana* Meyrick, originated from Australia and was first recorded in New Zealand, within the Auckland region, around 1921. This species is believed to be distributed throughout the country (Dugdale 1988). *S. macropetana* has been recorded on at least fifteen *Eucalyptus* species (Myrtaceae) in New Zealand, including *Eucalyptus botryoides, E. fastigata, E. nitens, E. obliqua, E. regnans* and *E. saligna* (Nuttall 1983).

This insect occurs primarily on juvenile foliage, but older leaves may also be attacked. *S. macropetana* larva forms the damaging life stage by feeding on the shoot tips, buds and developing flowers, which are adhered together with webbing. The insect shelters inside the resultant leaf roll, feeding on the plant tissue within, until the leaf becomes skeletonized and dies (Philips 1992).

S. macropetana inflicts damage on plantation forestry and to nursery stock and seedlings throughout New Zealand and Australia (van der Geest and Evenhuis 1991). Knowledge of pest lifecycles is vital to the development of pest management programs and to the correct identification of the different development stages. To date there has been no research carried out on the abundance and economic significance of *S. macropetana* on different plantation *Eucalyptus* species in New Zealand. This information is important for the selection of healthy tree species for plantation forestry. This paper reports on the life history and abundance of *S. macropetana* within the Manawatu and Bay of Plenty region.

METHODS

Insects

A laboratory colony of *S. macropetana* at Massey University (Entomology and IPM Laboratory), was maintained on freshly picked *Eucalyptus macarthurii* foliage at 20°C ± 2°C, 70% R.H, and a photoperiod of L:D 18:6. The colony was derived from insects collected from a Tasman Forest Industries *E. fastigata* and *E. nitens* plantation (Kawerau, Bay of Plenty) in November 1998.

Life history

Eggs of *S. macropetana* (n = 20) were individually inoculated onto *E. macarthurii* leaves and placed into individual transparent containers (10.1 x 8.5 cm). Each lid was modified with a 5 x 5 cm hole, covered with Tyvec mesh (10 x 10 cm). The foliage was cut so that two medium-sized leaves remained on each stem. Each stem was inserted into a small stopper vial (5 x 2 cm) containing water, then placed inside a container. The plant material was replaced when over half had been consumed by a larva or the leaves had lost their turgidity and colour.

Whilst in the pupal stage (n = 16), the individuals were sexed and paired. They were placed into containers as above, also containing sheets for an oviposition substrate (paper towelling, 5 x 5 cm) and a food source (5% honey solution). The food source was dispensed by an inverted test tube (5 x 2 cm) containing a sterile dental wick and was replaced every second day. All eggs laid on the paper were transferred to individual petri dishes (9 x 9 cm).

Every second day, age-dependent variables such as development stage, colour, weight, body length, head capsule width, number of eggs laid, number of eggs hatched, and sex, were recorded. Such information was used to ascertain the duration of each development stage and an overall development time, survival rate, sex ratio and fecundity on *E. macarthurii*.

Abundance

Five field sites were established within the Manawatu and Eastern Bay of Plenty regions. The sites were chosen on the basis of appropriate *Eucalyptus* species being present and the presence of juvenile foliage. The number of trees at the chosen sites varied from over 3000 to 70. Collectively, the site incorporated fifteen *Eucalyptus* species including *E. nitens, E. fastigata, E. brookerana, E. macarthurii, E. saligna, E. botryoides, E. obliqua, E. regnans, E. agglomerata, E. cladocalyx, E. pilularis, E. microcorys, E. baxteri, E. muelleriana* and *E. globoidea*. Each of the sites was visited three times over the 1998/1999-summer period. This equated to a separate site being visited each week over this time.

At the first visit, each field site was divided into four separate subplots. Each replicate contained the same host species and the same number of trees so that approximately 10% of the trees present at each site were examined at each visit. Therefore, the number of trees sampled differed between sites (range of 20 to 50 trees sampled per site). Parameters recorded from each tree included date, eucalypt host species, tree size, presence of adult foliage, old and current damage estimates, leafroller development stages present, and further comments. The number of incidences where two or more leafroller were present within the same webbing was recorded and converted to a frequency.

Abundance of *S. macropetana* was determined by a scale of 1-5. This was the approximate number of leaf rolls per tree: 1 = absent (0), 2 = scarce (1-5), 3 = moderate (6-10), 4 = abundant (11-20), 5 = severe (20+). The scale gave an indication of the level of infestation without opening every leaf roll on the tree. Each tree in the sample was scanned with the naked eye on each side for old and active webbing, and ~10 leaf rolls were randomly opened to ascertain development stage present.

The data were analysed for differences in abundance according to host species with a Kruskal-Wallis one way analysis of variance. Medians were separated using a pairwise multiple comparison using the Student-Newman-Keuls Method (SNK) ($P<0.05$).

RESULTS AND DISCUSSION

Life history

S. macropetana developed through five instars and had an overall developmental duration time of 46.2 ± 11.4 days (mean ± STD) under laboratory conditions (Fig. 1). The eggs were usually laid singly, but occasionally observed in batches of up to eight, and were laid on the underside of *Eucalyptus* leaves or paper towelling provided. The eggs ranged in colour from pale cream to brown as the 'blackhead' of the developing embryo became visible, and hatching occurred after a mean of 7.2 ± 0.5 days. Eggs were circular in shape and had an average width of 0.5 ± 0.05 mm.

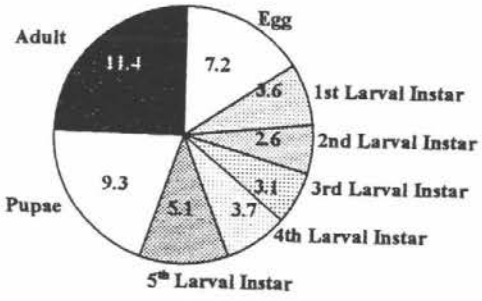

FIGURE 1: Mean duration (days) of different life stages in the lifecycle of *Strepsicrates macropetana* on *Eucalyptus macarthurii* at 20°C in the laboratory.

Measurements of larvae, which were then used to separate instars, are shown in Table 1. The early instars had a rounded black head and prothoracic shield, with a translucent green/grey body. Instars three and four had a brown head and prothoracic shield; the upper terga were medium green and exhibited pinnacula set in white dots with imminent dorsal setae. The anal shield was consistently square containing a distinctive dark 'U' shape in instars four and five. Male reproductive organs i.e. testes, became visible in the fourth instar. The final instar had a distinctive body colour ranging from yellow/brown to pink/red eminent before final eclosion. Overall, the pupation rate was 80%.

The pupae were characteristically contained within a silk cocoon inside a leaf roll or against other substrate. Pupae were golden yellow in colour after final larval moult, gradually becoming darker with age. The pupa had an obtect structure, with two rows of abdominal spines visible on the dorsal surface. The male pupa had four ventral abdominal segments visible and the female had three. The male pupa had an average weight of 1.17 ± 0.3 mg, and the female 1.46 ± 0.29 mg. The male pupa had an average length of 7.55 ± 0.98 mm and the female 7.16 ± 0.56 mm. The sex ratio was 2:3 M: F and 81% of pupae resulted in successful adult emergence.

S. macropetana showed sexual dimorphism in colouration, with the male having uniform ash/grey fore-wings, and brownish grey hindwings, which contained a fringe of hairs along the edge. The female had a lighter wavy band across the costa of the forewing. The adult rested with the wings held roofwise. An average fecundity was observed at 59 eggs per female, of which 94% hatched. The overall survival rate of the leafroller on *E. macarthurii* from egg to adult was therefore 65%. Adult sexual behaviour is currently under investigation.

When compared to other tortricid leafrollers, *S. macropetana* had a very similar life history. *Strepsicrates rhothia* Meyrick, a pest of several plant species including *Eucalyptus* and guava (*Psidium littorale*) had an average development time of 44 ± 2 days (mean ± SD) (Ahmad 1972). *S. rhothia* showed a maximum fecundity of 42.5 eggs per female and had up to eight generations each year. *S. macropetana* is believed to have at least two generations each year in the field, with the adults emerging in the spring and autumn (Miller 1925). Based on developmental time, we predict that further research will reveal that *S. macropetana* may go through many more generations than this, perhaps between 6 and 8, depending on climate.

TABLE 1: Measurements of different instar *S. macropetana* larvae on *E. macarthurii*.

Instar Number	Length (mm) Range	Mean	SD	Headcapsule width (mm) Range	Mean	SD
1	0.8 - 2.2	1.6	0.3	0.15-0.20	0.18	0.02
2	1.7 - 4.6	3.2	0.9	0.15-0.46	0.30	0.09
3	3.1 - 8.9	5.9	1.4	0.25-0.89	0.59	0.16
4	7.0 -11.9	9.9	1.1	0.50-1.26	0.97	0.16
5	10.5 -14.1	12.2	0.99	1.00-1.29	1.13	0.08

Abundance

S. macropetana damage was observed on all fifteen *Eucalyptus* species examined. The abundance of damage differed significantly between the *Eucalyptus* species examined (H= 52.5, df= 14, P< 0.0001). A comparison of abundance between different *Eucalyptus* species showed that *E. microcorys, E. nitens, E. fastigata* and *E. saligna* were highly susceptible to feeding damage by *S. macropetana* (Fig. 2). The species least susceptible to feeding damage were *E. cladocalyx, E. baxteri, E. muelleriana, E. obliqua, E. globoidea* and *E. regnans*.

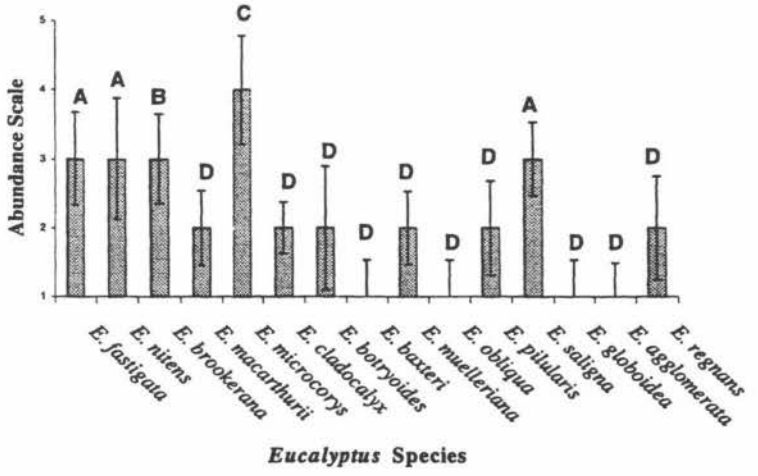

FIGURE 2: Influence of *Eucalyptus* host species on the abundance of *Strepsicrates macropetana* (scale of 1 absent to 5 severe) over one season in the Manawatu. Medians followed by the same letter are not significantly different at P = 0.05. Error bars represent the range of abundance on each *Eucalyptus* species.

The relationships between host species, the presence of juvenile foliage and/or climatic variation on *S. macropetana* abundance are currently under investigation.

The early larval instars typically occurred within buds, on shoot tips or between the apical junction of two leaves. Usually larva occur singly inside leaf rolls; however, two to six larvae were observed within the same webbing, at a frequency of 0.89% (n = 3430). The older larval instars tend to move away from the apical tips and further down the tree, commonly webbing together leaves. Pupa and adults have been observed inside leaf rolls or close to old larval damage.

The current research provides the foundation for further investigation into *Eucalyptus* leafroller phenology and behaviour.

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