The ecology of key arthropods for the management of *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) in Coonawarra vineyards, South Australia

Cate Paull

B.NRM – Hons, The University of Adelaide

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Australian Centre for Evolutionary Biology and Biodiversity
School of Earth and Environmental Sciences
The University of Adelaide
Australia

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Abstract

There is currently little knowledge about the dynamics of invertebrates in Australian viticultural ecosystems. This study was conducted in Coonawarra vineyards over three seasons (years) and has focused on identifying natural enemies, their seasonal phenology, multiple species interactions, and potential for the suppression of the pest lepidopteran *Epiphyas postvittana* (Tortricidae). The work presented in this thesis shows that endemic natural enemies have far greater potential to control *E. postvittana* than has been realised.

An initial survey identified a diverse and abundant range of potential natural enemies. Of these, the species most likely to attack *E. postvittana* include a predatory mite *Anystis baccarum* and a number of hymenopteran parasitoids. The most abundant parasitoid in the vineyards was a braconid, *Dolichogenidea tasmanica*.

Understanding the characteristic behaviour of parasitoids in response to host density can help to gauge their potential for pest suppression. The results of large-scale field experiments showed that the response of *D. tasmanica* to the density of *E. postvittana* was inversely density-dependent, and that parasitism was consistently higher in Cabernet Sauvignon compared with Chardonnay varieties.

Despite the fact that interactions among multiple species of natural enemies can increase or decrease pest suppression, particularly when they share a common prey/host, few multi-species interactions have been investigated. Laboratory studies identified a novel interaction between the predatory mite *A. baccarum* an abundant predator in the vine canopy, the parasitoid *D. tasmanica* and host *E. postvittana* larvae. Although *A. baccarum* readily ate *E. postvittana* eggs and free roaming larvae, they could not access larva in their silk leaf rolls. However, the addition of *D. tasmanica* significantly increased predation of *E. postvittana* larvae, by altering the behaviour of host larvae and increasing their vulnerability to the mite.

Experiments conducted at a landscape level in the Coonawarra showed that *D. tasmanica* was also present in habitat other than vineyards including native vegetation. However, it was not present in highly disturbed habitats. Although the exact mechanism for this remains unknown, results indicate that viticultural practices and resources in the surrounding landscape can influence the presence of parasitoids. Together, the findings presented in this thesis make a significant contribution towards developing sustainable pest management in Australian viticulture.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

Cate Paull

14 December 2007

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For My Dad
Torrance Paull
28.3.1925 – 13.11.2004

CHAPTER 1

General Introduction and Aims

1.1 INTRODUCTION

Natural pest control is an ecosystems service that is valued by humans (Mooney et al. 1995b, Wilby and Thomas 2002, Losey and Vaughan 2006). The necessary conditions that define ecosystem services are that they: 1) emerge from a natural environment, 2) enhance human well being, and 3) are an end product of nature directly used by people. There are numerous examples of native predatory arthropods and parasitoids that colonise crops and suppress pests, hence providing an important ecosystem service (Murphy et al. 1996, Lewis et al. 1998). There are also numerous challenges in maximising their pest control potential. Increasing natural enemy population densities and species diversity may influence their ability to suppress pest populations (Barbosa 1998, Bugg and Pickett 1998, Schellhorn et al. 1999, Landis et al. 2000). This can be achieved by increasing natural enemy colonisation into a crop, then maximising their reproduction and longevity. Greater species diversity of natural enemies may result in reduced pest populations, because each species kills a life stage of the pest that otherwise would have survived (Roland 1988, Holt and Lawton 1994, Symondson et al. 2002, Cardinale et al. 2003).

The native light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) is a major concern in Australian vineyards. One of the current objectives of the Australian wine industry is to reduce the levels of broad spectrum insecticides applied to viticultural systems, and to investigate the benefits of protecting and enhancing diversity of soil and above-ground arthropods, and the contribution they make to sustainable pest control practices (South Australian Wine and Brandy Industry Association Incorporated and Winemakers Federation of Australia 2002). This study identifies ways to enhance management of *E. postvittana* by determining its key natural enemies, how these enemies respond to *E. postvittana* feeding in different grape varieties and at varying densities, interactions among multiple species of natural enemies, and where they occur.

Epiphyas postvittana, a leaf rolling, polyphagous, multivoltine moth, causes damage by reducing grape yield during spring when larvae eat the shoots, flowers and young fruits (Danthanarayana et al. 1977, Danthanarayana 1983). Feeding damage from the larvae causes wounds in plant tissue, creating infection sites for disease and fungi such as *Botrytis cinerea* (Baker and Lang 1983, Buchanan and Amos 1988, Ferguson 1995). *Epiphyas postvittana*

over-winters in a quiescent state on a range of non-crop host plants (Danthanarayana 1975). Several authors suggest that larvae crawl from these host plants onto crops (e.g. apple and grape) to feed at budburst (Buchanan 1977, Baker and Lang 1983), although there is no experimental evidence to support this. Anecdotal information from local growers prior to this study indicated that *E. postvittana* occurs in larger numbers in some grape varieties, especially Chardonnay, compared with red varieties such as Cabernet Sauvignon. Until this study, no one had formally quantified this claim.

While much is known about the life history of *E. postvittana*, very little information is available about its predators and parasitoids in terms of species present, their basic biology, abundance, seasonality, interactions and potential level of mortality they cause to *E. postvittana* in Coonawarra vineyards. Clearly, research to identify the most appropriate natural enemies of *E. postvittana* (or pests in general) should include understanding:

- the natural enemy complex associated with the pest (e.g. DeBach and Rosen 1991, Waage and Mills 1992, New 1996);

- the response of natural enemies to host or prey density (e.g. Huffaker et al. 1976, Murdoch and Briggs 1996);

- the likely interspecies interactions between natural enemies (e.g. Holt and Lawton 1994, Murdoch and Briggs 1996, Cardinale et al. 2003) and

- the mechanisms that increase the survival, fecundity (Huffaker et al. 1976, Hawkins and Sheehan 1994, Casas 2000) and longevity of natural enemies and their availability, both spatially and temporarily (Murphy et al. 1996, Tscharntke and Kruess 1999a, Landis et al. 2000).

These four points are the focal research areas of this study.

1.2 NATURAL ENEMIES OF *Epiphyas postvittana*

Natural enemies are predatory arthropods or parasitoids that kill and consume other arthropods (pests or prey). Parasitoids include species of Diptera (flies) and Hymenoptera (wasps) that oviposit externally on or internally in a host, where eggs hatch, and larvae feed and develop into adults, killing the host (Van den Bosch et al. 1982, Landis et al. 2000).

There have been a number of arthropod species that have been recorded as preying on or parasitising eggs and larvae of *E. postvittana*. However, most of this information comes from anecdotal observations made while conducting research on the biology and behaviour of *E. postvittana* and from regions and crops other than the Coonawarra and grapes (Nicholls 1934, Dondale 1966, MacLellan 1973, Cordingley and Danthanarayana 1976, Farrugia 1976, Buchanan 1977, Danthanarayana et al. 1977, Danthanarayana 1980b, a, Farrugia 1981, Baker and Lang 1983, Baker 1983, Buchanan and Amos 1988, Baker and Bailey 1993, Glenn et al. 1997, Thomson et al. 2003).

1.3 NATURAL ENEMIES: RESPONSE TO HOST DENSITY

Natural enemies that operate in a density dependent manner are important in regulating populations (Cappuccino and Price 1995, Price 1997). Natural enemy colonisation and reproduction in response to host density can indicate their effectiveness as a pest control agent (Huffaker et al. 1976, Hawkins and Sheehan 1994, Murdoch and Briggs 1996, Casas 2000). Whether natural enemies respond to prey in a density dependent or independent manner has been discussed at length by numerous researchers (e.g. Krebs 1994, Cappuccino 1995, Dempster and Mc Lean 1998). One of the most successful examples of density dependent predation was for the winter moth *Operophtera brumata*, where it was shown that pupal predators operated in this manner (Varley et al. 1973).

Density dependent responses result from one of two characteristic behaviours from the predator, either as a functional or a numerical response (Solomon 1949). Functional response takes place when a predator kills more prey in response to increasing prey density. Numerical response occurs when an increase in prey density causes an increase in the numbers of predators available to attack the prey. This may be due to increased survival, reproduction or colonisation of predators (Holling 1961, Southwood and Way 1970, Price 1997). Density independent response of natural enemies has no relationship to prey density (Solomon 1949).

The reproductive numerical response is also the result of the natural enemy's functional response including searching efficiency, host specificity, and synchronicity with prey

(Murdoch and Briggs 1996). However, factors such as environmental parameters and host plant quality should also be considered as they are important (Levins and Schultz 1996).

It is generally accepted that the numerical response of predators is less than that of parasitoids because most predators have a broad host range, consuming alternative prey that may reduce their functional response as the density of a specific prey species increases (Sabelis 1992).

Specifically, there is little published information about the response of parasitoids to host density of multivoltine tortricids and what is available shows varied results (Newton 1988, Bezemer and Mills 2001, Sugiura and Osawa 2002). Research on *Goniozus jacintae*, a parasitoid of *E. postvittana*, showed a delayed inverse density-dependent response (Danthanarayana 1980b). However, there has been no published research on the response of the dominant parasitoid in the Coonawarra, *Dolichogenidea tasmanica*, to population density of *E. postvittana.*

1.4 MULTI-SPECIES INTERACTIONS

The complexity inherent in ecological processes underpinning biological control has meant that it is only relatively recently that the classic single focussed predator-prey interaction has been widened to include investigating multi-species interactions (Price et al. 1980, Rosenheim et al. 1995, Schellhorn and Andow 1999b, Cardinale et al. 2003, Fournier et al. 2003, Harmon and Andow 2003, Ives et al. 2005). There are a range of interactions, both direct and indirect, that take place between predatory species; predator-predator interactions (Schellhorn and Andow 1999a), predator-parasitoid (e.g.Colfer and Rosenheim 2001) and parasitoid-parsitoid (e.g.Perez-Lachaud et al. 2002), with a range of outcomes for pest suppression (Huffaker et al. 1984, Hurd and Eisenberg 1990, Sih 1993, Rosenheim et al. 1995, Losey and Denno 1998, Cardinale et al. 2003, Rosenheim et al. 2004).

The results of these interactions also depend on the type and behaviour of the prey. Insects have evolved numerous adaptations to defend themselves. These anti-predator strategies are evident in a number of different insect orders, including lepidopteran larvae (Fukui 2001, Gentry and Dyer 2002). Biting, dropping and regurgitating are direct responses used by lepidopteran larvae against attack by parasitic Hymenoptera (Gentry and Dyer 2002). Silk used by larvae in leaf rolls and ties may also offer increased protection against predation (Damman 1987). However, there has been little work undertaken to establish the interaction among multiple species of natural enemies and specific host defences and interactions with other species in vineyard agro-ecosystems.

1.5 FACTORS INFLUENCING THE ABUNDANCE OF NATURAL ENEMIES

Agricultural ecosystems in the western world are often large areas dominated by relatively few crop species (Southwood and Way 1970), where reduction in diversity of the primary trophic layer can have a negative effect on ecological processes (Denys and Tscharntke 2002). These systems are characterised by continuous abiotic disturbances. These disturbances are usually the result of various management activities that are undertaken to promote the growth and productivity of crops, including the use of chemicals to control diseases and weeds as well as slashing, pruning, trimming and harvesting. Such intense agricultural practices can reduce natural enemy diversity in agroecosystems (Wilby and Thomas 2002).

Survival, fecundity and longevity of natural enemies are dependent on and influenced by various resources. They include food containing specific nutrients and amino acids essential for reproduction (Hagen 1987), vegetative structure (Langellotto and Denno 2004a) or shelter for over wintering, refugia from agricultural chemicals (Martinsen et al. 2000, Horton et al. 2002), or when alternative prey/hosts are in low numbers or unavailable (Doutt and Nakata 1973). These resources are not always spatially or temporally available, especially in agricultural systems, and often there are a number of mechanisms at work at the same time (Landis et al. 2000).

Determining the specific mechanism influencing natural enemies in the system of focus is an important first step in identifying factors that can be modified in order to enhance their effectiveness (Andow 1991, Corbett and Plant 1993, Schoenig et al. 1998, Huffaker et al. 1999, Schellhorn et al. 1999, Kennedy and Storer 2000, Landis et al. 2000).

Habitat fragmentation results in discontinuous spatial patterns and isolated patches that impact and influence the interactions and dynamics among organisms (Tscharntke and Kruess 1999a). Fragmentation may reduce accessibility to alternative food resources, therefore it is important to consider the pattern of resources, the distance between them, and the mobility of natural enemies that use them (Landis et al. 2000). Evidence suggests that specialist natural enemies such as parasitoids are more easily disturbed and can become locally extinct when the landscape is fragmented (Thies and Tscharntke 1999, Kruess and Tscharntke 2000, Wilby and Thomas 2002).

Studies on colonisation, fragmentation and disturbance have led to increasing research to try and understand how natural enemies perceive resources at a range of spatial scales, and how they move among different crop and non-crop habitats at local and regional levels (Kennedy and Storer 2000, Thompson et al. 2001, Elliott et al. 2002, Schellhorn and Andow 2005). For

some part of the year many crops are either dormant or land is left fallow. With little to support populations of natural enemies, these ecosystems rely on insect recolonisation (Tscharntke and Kruess 1999a). Therefore, successful colonisation of an area by natural enemies will depend on the ability of an adjacent area to support large and persistent poulations of natural enemies (Schellhorn et al. 1999). Also, the likelihood of recolonisation diminishes with smaller patch sizes and with increasing patch isolation (Hanski 1998).

Investigating whether or not parasitoids are successful in areas outside of vineyards may indicate the factors responsible for their success; these could then be replicated in areas where the services of natural enemies are required. However, this approach has to be balanced with the notion that these same habitats could also provide sources of colonising pests. This information can then be used to design contemporary management practices 'conservation biological control', 'restoration of ecosystems' and 'ecological engineering' to manipulate environments to either sustain, increase or reinitiate these processes and services, for example the biological control of pests (Barbosa 1998, Landis et al. 2000, Thompson et al. 2001).

These concepts of resource provision, fragmentation, colonisation, source-sink dynamics at the landscape level, and anthropogenic disturbance, may apply to the perennial grape-growing ecosystem of the Coonawarra. Grape vines are dormant over winter, therefore predators and parasitoids are likely to immigrate into the vineyards from sources at the beginning of each season. Whether they persist will be dependent on numerous factors such as prey and mate availability, and the degree of disruption caused by agricultural management practices.

There are no records of *E. postvittana* causing damage to native vegetation. However, there are several species of native parasitoids of *E. postvittana* which attack it in grape vines (see Chapters 2 and 3). Further, there has been no research to investigate the biology or habitat management requirements for any of the natural enemies associated with *E. postvittana*.

1.6 AIMS OF PROJECT

Given that very little is known about the natural enemies that attack *E. postvittana*, this was an initial focus of the current study. Chapter 2 describes the diversity of predatory and parasitic arthropods in Coonawarra vineyards that potentially feed on vineyard pests such as *E. postvittana* and where they are found.

Chapter 3 deals with the relative abundance of *E. postvittana* larvae and levels of parasitism for three consecutive seasons (2002-05), in Chardonnay, and for one season (2004-05) in both Chardonnay and Cabernet Sauvignon grape vines. This chapter also provides the basis for the experimental work presented in subsequent chapters.

Chapter 4 examines whether parasitism of *E. postvittana* by the most abundant parasitoid, *Dolichogenidea tasmanica* is density dependent in different grape varieties and across vineyards. Two approaches were used: first by inoculating *E. postvittana* larvae at high and low densities, and second by using naturally occurring larval populations that varied in density.

In Chapter 5, after making the observation that the predatory mite, *Anystis baccarum*, was a voracious predator of *E. postvittana* larvae, two experiments were conducted. First, to determine whether this predatory mite could enter silk shelters and prey on *E. postvittana* and, second, to determine the outcome of the multi-species interaction among the predator, *A. baccarum*, the parasitoid, *D. tasmanica*, and the prey/host, *E. postvittana*.

The aims of Chapter 6 were to determine: 1) whether the most abundant parasitoid, *D. tasmanica* occurs in areas of native vegetation in the Coonawarra region, 2) if there is an association between *D. tasmanica* and the level of disturbance in different areas, and 3) early in the grape growing season where does *D. tasmanica* first occur, in the vineyards or native vegetation?

In Chapter 7 the key findings of this study are reviewed and integrated, and a general discussion is presented on the impact these results are likely to have on the future management and research leading to a reduction in chemical insecticides, and in developing sustainable management strategies for *E. postvittana*.

CHAPTER 2

Identifying Natural Enemies from Coonawarra Vineyards for the Management of *Epiphyas postvittana*

2.1 INTRODUCTION

One of the current objectives of the Australian wine industry is to reduce the levels of broad spectrum insecticides applied to viticultural systems, and to investigate the benefits of protecting and enhancing diversity of soil and above-ground arthropods, and the contribution they make to sustainable pest management practices (South Australian Wine and Brandy Industry Association Incorporated and Winemakers Federation of Australia 2002). The key insect pest in southern Australian vineyards is the native insect *Epiphyas postvittana,* light brown apple moth. This species causes reduced grape yields during spring when populations of *E. postvittana* larvae eat the shoots, flowers and young fruits. Feeding damage causes wounds in plant tissue, creating infection sites for disease and fungi such as *Botrytis cinerea* (Baker and Lang 1983, Buchanan and Amos 1988, Ferguson 1995). *Epiphyas postvittana* is a major concern to Coonawarra vignerons. While much is known about the life history of *E. postvittana*, very little information is available on the other species present, their abundance, seasonality and to what degree natural enemies contribute to the mortality of *E. postvittana*.

Beneficial arthropods (also known as 'natural enemies') are considered to be predatory arthropods, i.e. insect predators that kill and consume other arthropods (pests or prey), and parasitoids, mostly Diptera (flies) and Hymenoptera (wasps), that oviposit their eggs on or into the egg, larval or pupal stage of an arthropod species (the host). The egg hatches and the resultant parasitoid larvae feed from the outside or within the host eventually killing it (Van den Bosch et al. 1982, Landis et al. 2000). There are numerous well-documented cases where predatory arthropods and parasitoids have been used to help suppress or control insect pests (Murphy et al. 1996, Settle et al. 1996, Gerson et al. 2003). Often referred to as 'biological control' or 'conservation biological control', this is an important part of integrated pest management (IPM) programs.

The main aims of this section of the project were to document the diversity of predatory and parasitic arthropods that would potentially feed on vineyard pests such as *E. postvittana*. In order to determine the most abundant groups of predators and establish general baseline information about the arthropod community in vineyards, a survey was conducted in the first

year of the project. Arthropods captured were identified as natural enemies based on their taxonomy, biology or morphology of their mouthparts. To investigate the parasitoid diversity associated with *E. postvittana*, eggs, larvae and pupae were also collected and reared through which culminated in a national revision of the hymenopteran parasitoids associated with *E. postvittana* (see Appendix 2).

2.2 MATERIALS AND METHODS

The invertebrate survey was conducted in the Coonawarra region, situated 370 km south-east of Adelaide, South Australia (Figure 2.1). Although the region has an international reputation for producing fine wines, up until the early 1960's there was only a total of 450 ha of vineyard. Currently vineyards are grown in a concentrated area covering 5000 ha between the townships of Penola and Coonawarra, an area 20 km long and approximately 2 km in width (Figure 2.2). Underlying this area is terra rossa soil, which is predominantly clay-based soil overlying limestone. The topography is characteristically flat with an elevation of approximately 60 m above sea level. The average annual rainfall is 590 mm (Figure 2.3).

NOTE: This figure is included on page 22 of the print copy of the thesis held in the University of Adelaide Library.

Figure 2-1 Map of Australia with inset of South Australia highlighting the Coonawarra grape growing region (Australia Geoscience 2007).

Figure 2-2 Aerial view over the northern section of the Coonawarra region.

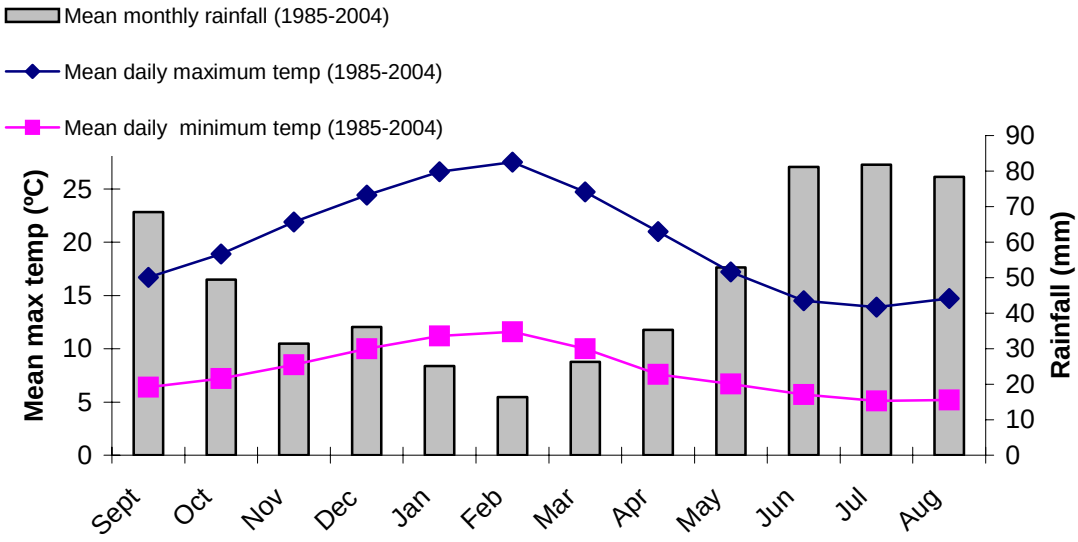


Figure 2-3 Average minimum and maximum temperature and rainfall for the Coonwarra region (Australian Bureau of Meterology 2007).

2.2.1 Sites

Arthropod sampling was conducted at five vineyards (sites) in the Coonawarra: Balnaves (37º20' 825S 140º50' 821E), Kidman (37º20' 922S 140º51' 448E), Messenger (37º21'337S 140º50' 107E), Provis (37º12' 970S 140º52' 579E) and Rymill (37º14' 529S 140º49' 066E). The Balnaves, Kidman and Messenger sites were approximately 1 km away from each other. The Rymill and Provis sites were 15 km NNW and 20 km NNE away from the previous three sites.

Vineyards at all five sites were similar in respect to vine age (10 years, except Rymill -15 years), rootstock, variety (Chardonnay), disease management, and average shoot number. The Balnaves, Kidman and Messenger sites were characterised by a conventional vineyard management regime. For example, the type of chemicals used and frequency of their use at these three sites for the control of diseases and pests were similar and reflected management that was typical across most Coonawarra vineyards. There were some differences between the sites these included surrounding land use, pest control and midrow management.

The Provis site was atypical in regard to surrounding land use. This site was bordered by 80 ha of native vegetation to the east, *Pinus radiata* forest to the north, and intensive horticulture potato and onion to the north-west.

For the control of *E. postvittana* all sites used Dipel® however, Balnaves, Kidman and Messenger sites also used Avatar®. Rymill also used *E. postvittana* pheromone lures.

The midrow at Balnaves consisted of phalaris grass, at Kidmans was volunteer sward, and at the Messenger and Rymill sites the midrow was predominantly contiguous ryegrass with some volunteer broad leaf weeds such as *Plantago* sp., brassicas and *Centaurea nigra* (black knapweed). However, these weeds contributed to less than 3% of total cover. The midrow at Provis comprised a sparse covering of volunteer broadleaf weeds *Oenthera glazioviana* (evening primrose), *Marrubium vulgare* (horehound) and some brassicas.

2.2.2 Arthropod Trapping Methods

There are many different types of traps that can be used to sample arthropods. Each type of trap has advantages and disadvantages depending on factors such as habitat and focus species (Lindgren 1983, Bruck and Lewis 1998, Prokopy et al. 1999, Riecken 1999, Katsoyannos et al. 2000, Amalin et al. 2001). While a number of methods were used for this survey, a number of methods were also discounted. This was because they are specific to a particular group or to groups that were not considered beneficial, or they attract individuals over too great a range

(i.e from outside the vineyards), or they were likely to catch large numbers of individuals and over-extend the process of sorting and identification. After careful consideration and preliminary trials, the following trapping methods were used and were replicated four times at each site, except for visual searching.

Pitfall traps: These are the most widely used method for sampling ground- and litter-dwelling arthropods (Greenslade and Greenslade 1971, Spence and Niemela 1994, Standen 2000). They were made out of a 7 cm diameter PVC plastic sleeve that was buried flush with the ground surface. A plastic cup (200 ml) was inserted into each sleeve and half filled with weak saline and detergent solution.

Yellow pan traps: These are used to trap highly mobile, flying insects. They consisted of yellow plastic trays (21 cm wide, 30 cm long, 9 cm deep). Trays were filled with the same solution as for the pitfall traps, and were loosely covered with wire mesh to reduce disturbance from vertebrates.

Funnel samples: These were collected using a large plastic funnel (37 cm in diameter) that was held directly under the cordon of the vine while the cordon was hit five times from above using a rubber mallet. This was a modified version of the funnel method used by Costello and Danne (1997).

Visual searching: *E. postvittana* larvae were collected by searching for their conspicuous leaf rolls in the canopy for 30 min at each site. Life stages were collected and placed into individual rearing containers and monitored until they had completed their development.

Spacing of vine rows and panels were the same for the five sites. Vine panels consist of a number of grape vines (usually 3-4) between two trellis posts. Trellis posts were evenly spaced at 6 m throughout the vineyard and rows were 3 m apart. A single panel consisting of three vines only was randomly chosen for each trap position and this provided a convenient grid for standardising trap placement. Positions were randomised and no position was used more than once. Each vineyard was sampled every month for 12 months from September 2002 to August 2003. All traps (except for funnel samples) were exposed for 72 h before they were collected. The contents of traps were strained through nylon voile into 70% ethanol, with traps and strainers being rinsed and back washed with 70% ethanol. Due to time constraints priority was given to sorting samples collected from four months during the grapevine growing season; September, November, January and March.

Arthropods were sorted to order and morphospecies, with each individual being uniquely identified by site, trap type, and position. Further identification was guided by the biology of known families and whether or not they had predatory mouthparts. Some common predator and parasitoid species were accurately identified by Dr Ian Gauld from the Natural History Museum with priority based on the likelihood of a biological association with *E. postvittana*.

2.2.3 Identifying Parasitoids of *Epiphyas postvittana*

Collecting and rearing of field collected hosts is one of the best ways of confirming a host parasitoid association (e.g. Gauld and Bolton 1988, Shaw 1997). To identify the parasitoids associated with *E. postvittana*, collection and rearing of life history stages of *E. postvittana* from grape vines was undertaken in parallel to the arthropod survey, and included collections from roadside, native vegetation and vineyards during subsequent field experiments conducted in the Coonawarra region between December 2002 and January 2005 (see Chapters 3, 4 and 6). Eggs, larvae and pupae were collected from host plants, returned to the laboratory and held at 24°C. Host stages were placed in individual rearing cages and provided with foliage, and development was recorded for individuals every second day until any parasitoids emerged.

2.3 RESULTS

2.3.1 Abundance by Order

Because of extreme variance among traps and trap types, the resulting data were pooled. This yielded 42,658 individuals comprising 17 orders and 583 morphospecies (see Appendix 1). Collembola were the most abundant order contributing to > 60% of individuals, followed by Hymenoptera, Diptera, Hemiptera and Thysanoptera. The remaining 12 orders contributed only 7% of individuals (Figure 2.4). Natural enemies were represented in seven of the 17 orders, i.e. Hymenoptera, Diptera, Acarina, Coleoptera, Araneae, Dermaptera and Neuroptera.

2.3.2 Trapping Methods

Yellow pantraps contributed the greatest number of morphospecies (475 or 81.4 %) including 326 hymenopteran morphospecies (Figure 2.5a). Pitfall traps contributed the second greatest number of morphospecies 130 (Figure 2.5b), followed by funnel sampling of the vine canopy 31 (Figure 2.5c) and visual searching (22 morphospecies) (Figure 2.5d). Very few of the morphospecies captured using the funnel method were trapped using other methods. Even though there was some overlap, there was clear distinction between the biology of groups of arthropods and the type of trap they were caught in. This is evident when considering the spiders (Table 2.1) where web builders, species of Araneidae associated with foliage were mostly caught in yellow pan or funnel traps compared with ground-inhabiting, hunting, spiders such as Salticidae and Sparassidae most of which were caught in pitfall traps. Similarly pitfall traps collected other ground active arthropods such as predatory carabids. While foliage active coccinellids and flying insects such as Hymenoptera were collected in large numbers in yellow pantraps.

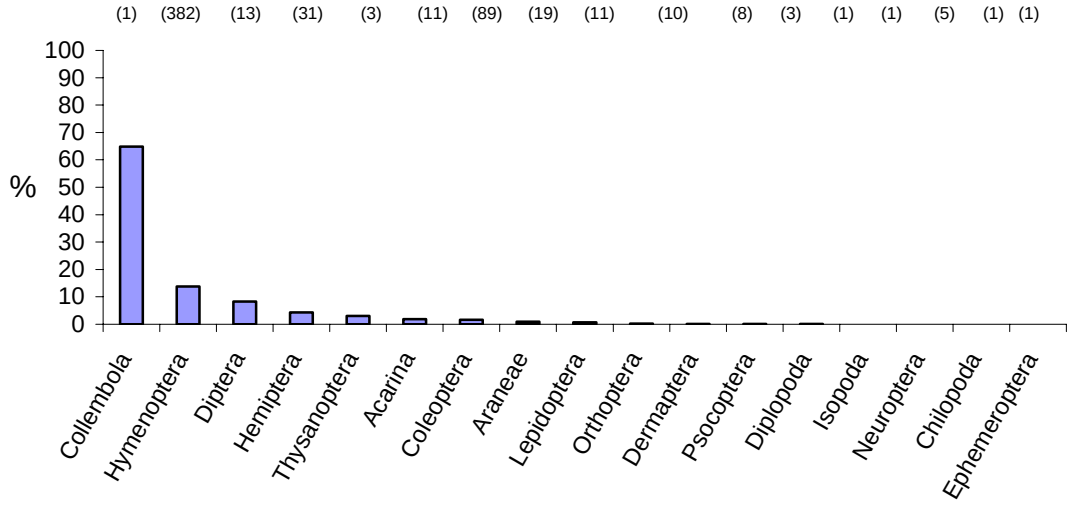


Figure 2-4 Percentage of the total number of individual arthropods for each order. The number in brackets is the number of morphospecies recorded for each order.

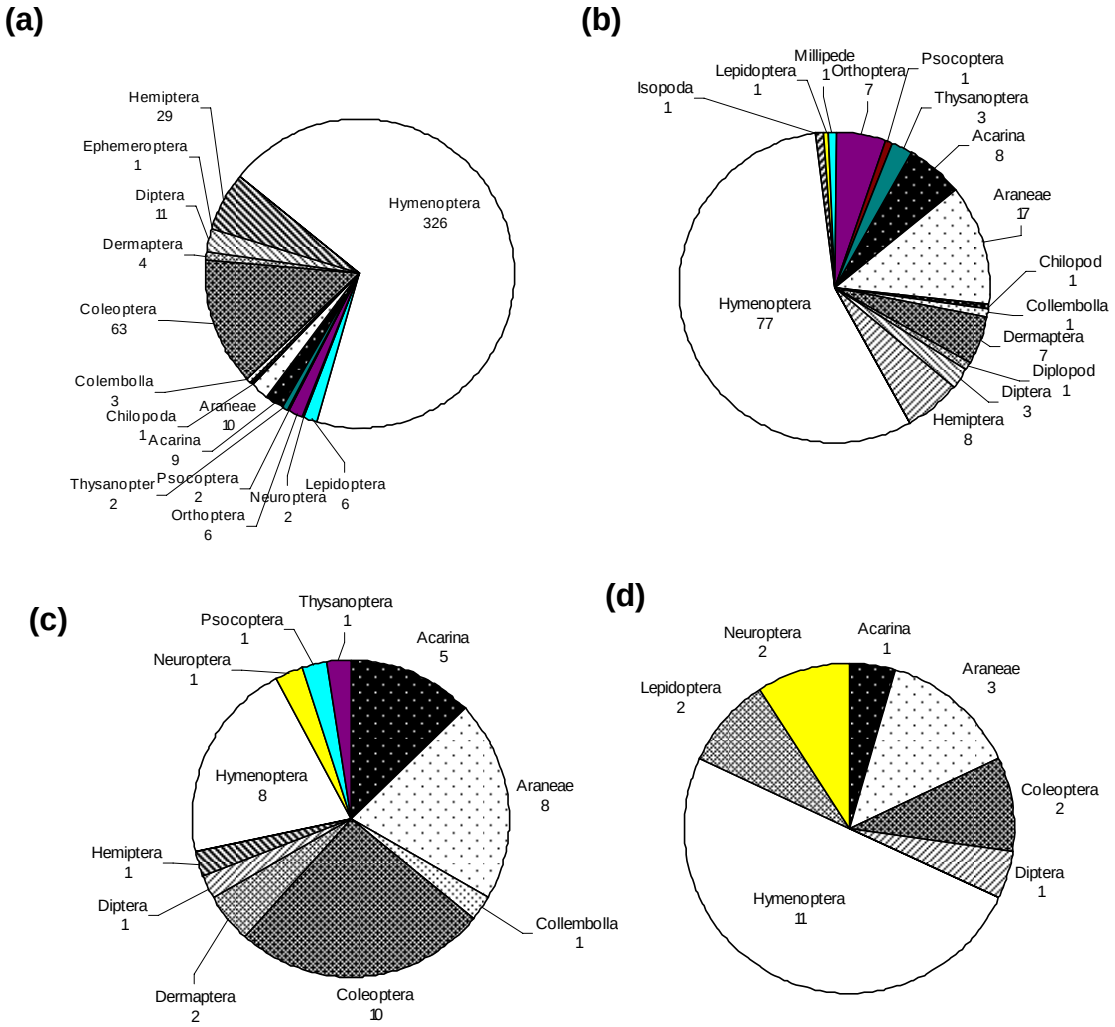


Figure 2-5 Percentages of morphospecies for each order collected from **(a)** yellow pantraps, **(b)** pitfall traps, **(c)** funnel samples and **(d)** visual searching. The number under each order is the number of morphospecies recorded.

Table 2-1 Summary of Araneae collected for all traps showing habitat, mode of predation and sample method. Hunter = active hunter, Web = web builder, Ambush = ambush predator. Undetermined morphospecies comprised juvenile instars that could not be indentified to family.

Morpho-species No.	Family	Habitat	Behaviour	Total	Pit	Pan	Fun
ARA454	Araneidae	Foliage	Web	7	0	1	6
ARA385	Araneidae	Foliage	Web	3	1	2	0
ARA475	Araneidae	Foliage	Web	2	0	2	0
ARA061	Clubionidae	Foliage	Hunter	41	9	27	5
ARA395	Dictynidae	Foliage	Web	1	1	0	0
ARA223	Mimetidae	Foliage	Hunter	13	4	9	0
ARA209	Pisauridae	Foliage	Hunter	1	1	0	0
ARA218	Thomisidae	Foliage	Ambush	2	0	1	1
ARA256	Gnaphosidae	Ground	Hunter	15	1	14	0
ARA046	Lycosidae	Ground/Foliage	Hunter	24	18	5	1
ARA483	Salticidae	Ground/Foliage	Hunter	7	0	5	2
ARA093	Salticidae	Ground/Foliage	Hunter	20	8	9	3
ARA054	Sparassidae	Ground Foliage	Hunter	39	30	9	0
ARA183	Zodariidae	Ground/Burrow	Hunter	1	1	0	0
-	undetermined	-	-	87	67	18	2
Total				263	141	102	20

2.3.3 Diversity and Abundance of Predatory Groups

2.3.3.1 Hymenoptera

The Hymenoptera were the most speciose order with 382 morphospecies across all trap types. Among the Hymenoptera the most abundant predatory groups were the Formicidae (ants, 58%) and parasitic Hymenoptera (16%). Parasitic Hymenoptera were the most speciose consisting of 300 morphospecies, comprising seven superfamilies and 41 families (Appendix 1). Of these, the most speciose superfamilies were Chalcidoidea and Platygasteroidea, consisting of 99 and 65 morphospecies, respectively (Figure 2.6).

The Formicidae was the most abundant predatory hymenopteran group comprising 58% of all Hymenoptera and 38 morphospecies. The most abundant subfamily of ants was Dolichoderinae (Figure 2.7), followed by Ponerinae, Formicinae and Myrmeciinae. In general, ants belonging to these subfamilies are considered general predators and scavengers and, although some species of *Pheidole* (subfamily Myrmicinae), are associated with harvesting seeds, they are also considered general predators (Shattuck 1999). The morphospecies *Iridomyrmex* sp. (HYM017) was the most temporally abundant for three of the four sampling periods and was recorded from all three types of traps (Figure 2.8).

2.3.3.2 Coleoptera

The second most speciose group was Coleoptera comprising 89 morphospecies. Predatory Coleoptera were represented by the families Staphylinidae, Coccinellidae and Carabidae, and these contributed to 20% of all beetles, and comprised 23 morphospecies. The most speciose of these was Coccinellidae with 10 morphospecies, followed by Carabidae (8 morphospecies) and Staphylinidae (5 morphospecies.). *Sarticus discopunctatus* (COL7) was the most abundant carabid and was found at each site and was present at all four sampling dates (Figure 2.9a). Abundance of coccinellid species varied throughout the season (Figures 2.9b). Staphylinids were more abundant early in the season, except for COL17, but decreased as the season progressed (Figure 2.9c).

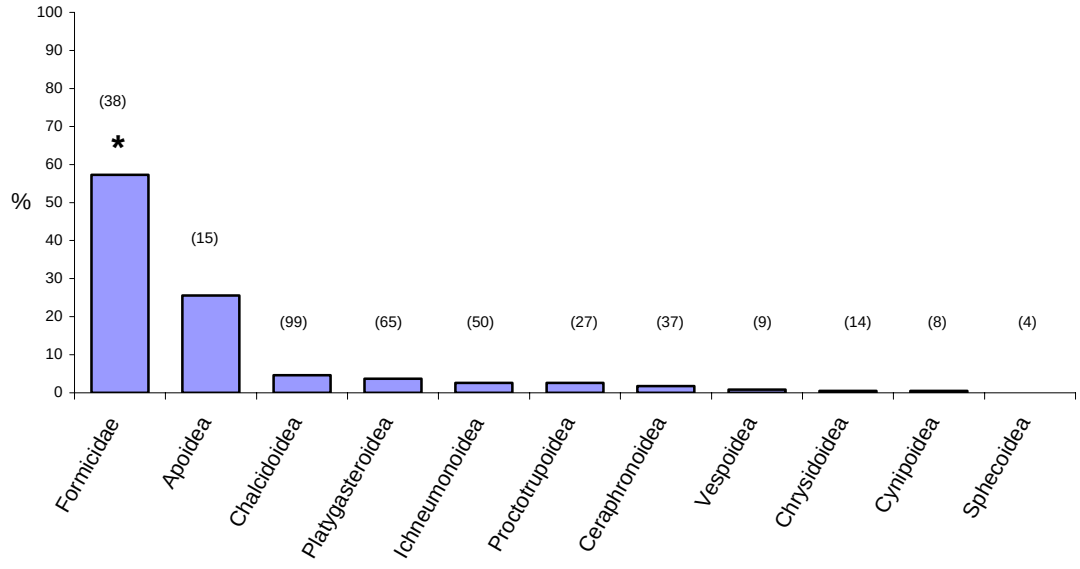


Figure 2-6 Percentage of individuals recorded for each hymenopteran superfamily for all traps combined. The number in brackets is the number of morphospecies recorded for each superfamily. *Formicidae have been separated from other Vespoidea to highlight their abundance relative to other groups.

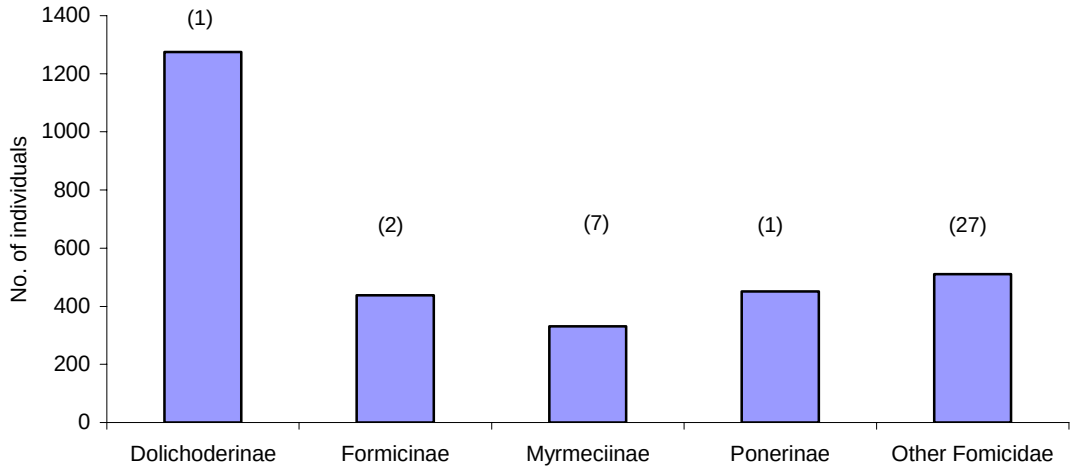


Figure 2-7 Abundance of individuals belonging to the four most common subfamilies of Formicidae pooled across all traps. The number in brackets is the total number of morphospecies recorded for each family.

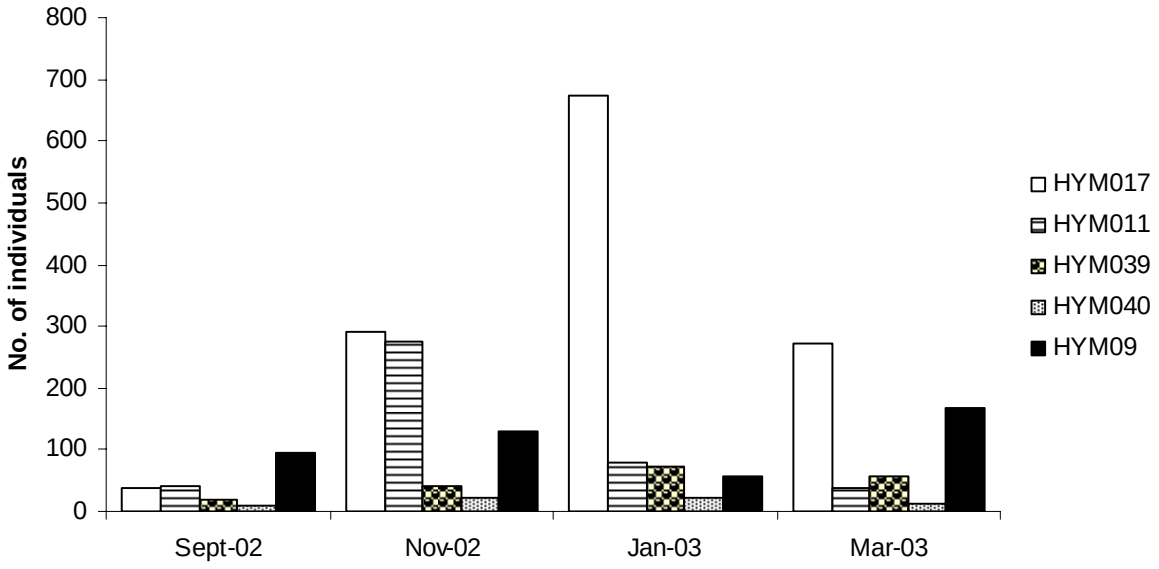


Figure 2-8 Temporal abundance of the five most common formicid morphospecies pooled across all traps for six months (Sept 02-March 03)

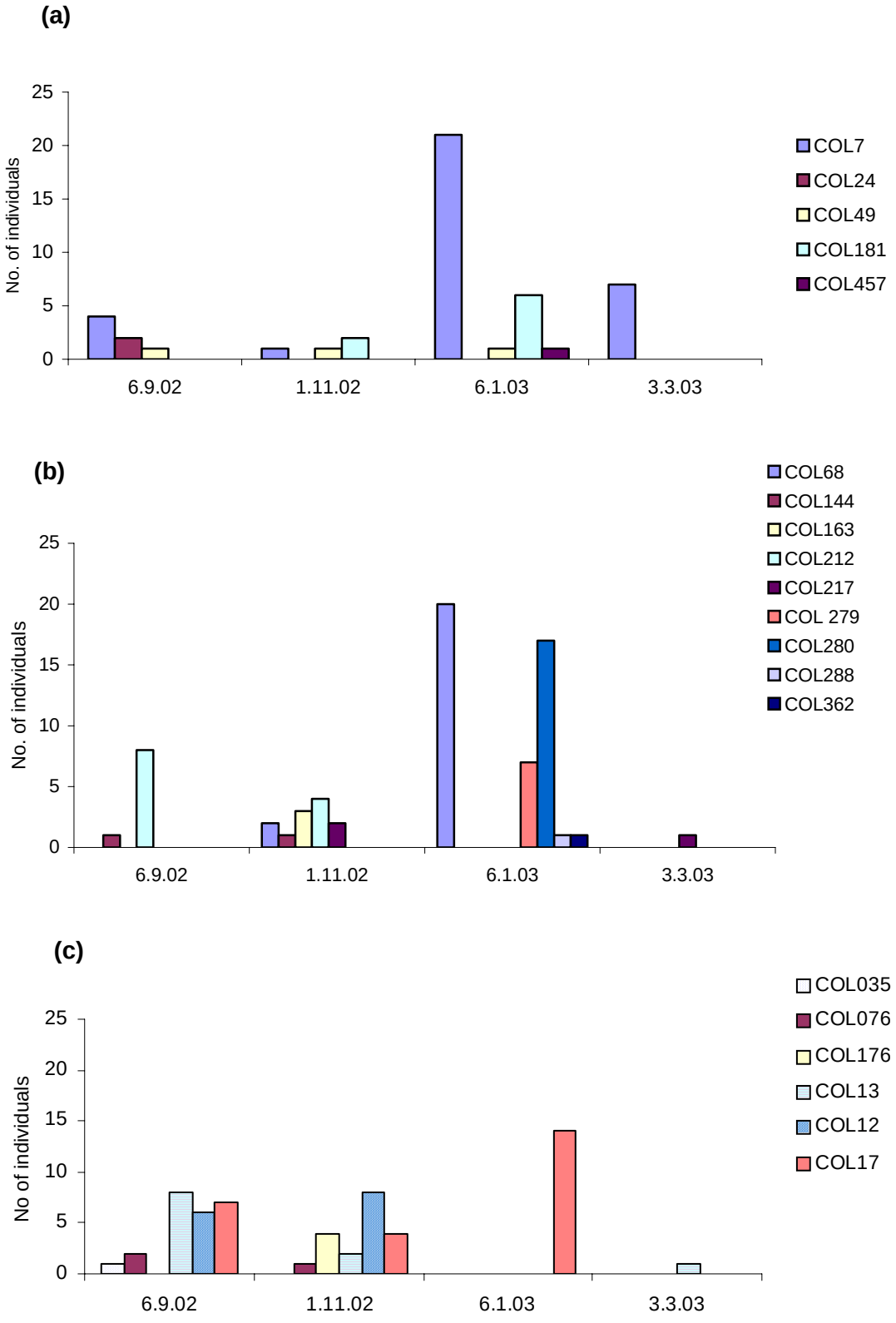


Figure 2.9 Temporal abundance of the most common **(a)** Carabidae, **(b)** Coccinellidae and **(c)** Staphylinidae morphospecies pooled across all traps for six months (Sept 02-Mar 03).

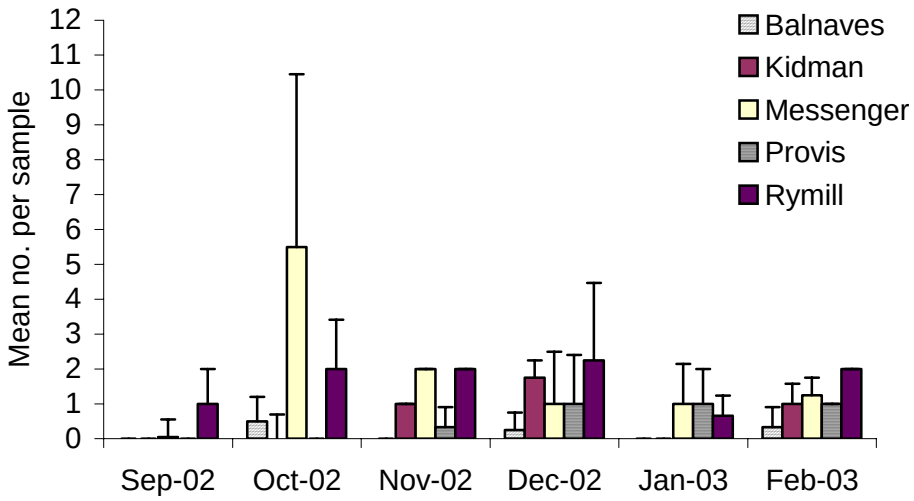


Figure 2-10 Mean number of *A. baccarum* (Acarina) captured for each funnel sample at each site for six months (Sept 02-Feb 03).

2.3.3.3 Other Predators

One of the most abundant predators found in the vine canopy was the predatory mite *Anystis baccarum*. Although numbers of this species varied across sampling periods, it occurred at all sites and often throughout the season (Figure 2.10). Predatory Acarina (mites) comprised 22% of the mites.

Araneae (spiders) are exclusively predatory; they contributed 0.04%, to the total number of arthropods. Spiders consisted of 14 morphospecies while the 13 orders other than Hymenoptera, Coleoptera and Hemiptera, each had 13 or less morphospecies. There were 14 species of spiders which could be divided into three distinct guilds, active hunters, web builders and ambush predators (Table 2.1).

Although Diptera were abundant, predatory taxa contributed less than 3% to the total number of flies. Within the Dermaptera (earwigs) less than 1% were predatory. Neuroptera (lacewings) are exclusively predatory; they also contributed less than 1% to the total number of arthropods. The Hemiptera consisted of 31 morphospecies however none were predatory.

2.3.3.4 Parasitoids of *Epiphyas postvittana*

Intensive collecting and rearing of *E. postvittana* larvae during 2002-2005 revealed that this host was parasitised by 12 species in the Coonawarra region, comprising 11 hymenopteran species and a single species of tachinid fly, *Voriella uniseta*. Several Hymenoptera were newly recorded from this host including, *Perilampus* sp. (Perilampidae), and six species of Ichneumonidae: *Euceros* sp., *Labium* sp., *Netelia* sp., *Plectochorus* sp., *Temalucha minuta* (Morley) and *Eriborus epiphyas* sp. n., the latter species being described in full. These results have been published separately as part of a national revision of the hymenopteran parasitoids associated with *E. postvittana* that includes an illustrated key for 25 species of parasitoids and hyperparasitoids, along with information on the taxonomy, identification, distribution and biology of each species. The details of this part of the study are presented here as Appendix 2. The abundance of these parasitoids from Coonawarra vineyards for each season of the study is presented in Chapter 3.

2.4 DISCUSSION

Prior to this survey the arthropods present in Coonawarra vineyards were largely unknown. This survey provides evidence that there is a relatively diverse and abundant range of predatory arthropods and parasitoids which are associated with *E. postvittana*, and have the potential to contribute to the control of this host.

Although all expected predatory arthropods groups were present in the Coonawarra there was a noticeable absence of predatory Hemiptera. Previous studies in vineyards have recorded a number of species including *Oechalia schellenbergii* and *Nabis* sp. (Cordingley 1981, Baker and Lang 1983, Daane and Williams 2003, Bernard et al. 2006), and the absence of these is somewhat perplexing.

The criticism is sometimes made that invertebrate surveys are often not conducted over long enough periods to reflect patterns of abundance that may be associated with crop phenology, seasonality or specific management practices (Duelli et al. 1999). Given that the survey undertaken here was conducted over twelve months, but only four months of data is presented, this criticism is probably partly valid. However, the overall aim of the survey was more so to achieve a snap-shot of the diversity and abundance of arthropods across growing seasons of vines to provide baseline information to underpin the more focused aspects of the study.

2.4.1 Trapping Methods

The combination of traps used for the survey indicated that some groups/species were associated with specific parts of the vine. For example, pitfall traps target ground active

arthropods such as hunting spiders and predatory beetles; funnels sampled extra taxa associated with the canopy; while yellow pan traps mostly collected flying insects, because this colour can act as a stimulus or attractant, particularly for Hymenoptera and Diptera (Southwood and Henderson 2000, Kevan et al. 2001). Many natural enemies feed on a variety of prey, but many also feed on various plant tissues such as pollen (Gilbert 1985), nectar (Bugg et al. 1987, Pemberton 1993, Idris and Grafius 1997, Winkler et al. 2006) or foliage (Ruberson et al. 1986). Vineyards are largely devoid of flowering plants, so yellow pantraps may attract more species because there few flowers and therefore reduced competition between flowers and traps (Hickman et al. 2001). Yellow pan traps also caught a number of ground predators, possibly because they are attracted by the water or struggling prey in the trap.

Comparison of trap efficacy can be difficult due to the different methods used and length of time the traps were exposed in the field. For example, pitfall and pantraps were static and caught arthropods over 72 hr compared to the relatively short period for timed searches and funnel trapping. Although the latter trapping method can provide an accurate measure of the species that are active in the vineyard canopy, it is likely to have underestimated highly mobile species such as wasps, flies and lacewings (Costello and Daane 1997, Morris et al. 1999). Importantly, funnel trapping did reveal the presence of the mite *A. baccarum* which turned out to be an important predator of *E. postvittana* and was used in subsequent experiments (see Chapter 5).

Visual searches are also likely to underestimate morphospecies in the canopy because of the cryptic nature of many groups, particularly immobile taxa. However, this method was most important for collecting *E. postvittana* larvae and revealed a diverse and abundant community of parasitoids associated with this host.

2.4.2 Predators and Parasitoids

Hymenoptera were clearly the most diverse and abundant group of predators in the Coonawarra, with Formicidae being the most numerous predatory group. One species (HYM17), *Iridomyrmex* sp., was collected in all trap types and at all sites. This result is not surprising as members of this genus are general scavengers and often dominate in Australian environments, often out competing all other arthropods (Greenslade and Halliday 1983, Shattuck 1999).

The characteristic biology of specific predators may mean that some species are more likely than others to prey on *E. postvittana*. For example, *Sarticus discopunctatus* was the most abundant carabid collected in vineyards and carabids are known to contribute to the control of

various pests (Lang and Gsodl 2001). However, most carabids are ground dwelling and it is therefore unlikely that this species would have a direct impact on *E. postvittana* present in the vine canopy. To be considered a potential predator for *E.postvittana,* a direct association between pest and predator should be established. This also includes establishing whether or not the predator is likely to be in the right habitat at the same time as *E. postvittana*.

Parasitic Hymenoptera were the most speciose group revealed by the survey and, again, this is not surprising given they parasitise a great range of insect hosts (LaSalle and Gauld 1993). The Chalcidoidea was the most speciose superfamily, a finding similar to other studies from olive and vegetable systems (e.g. Morris et al. 1999, Stephens et al. 2006). However, many species in this group are highly mobile and so are likely to be transient visitors associated with hosts found in other habitats (Levins and Wilson 1980). The diversity of parasitoids, their specialised biology and high degree of host specificity are the major reasons parasitoids have been utilised for controlling pests (Greathead and Greathead 1992, LaSalle and Gauld 1993, Mills 2000, Shaw 2006). Determining which parasitoids had a direct association with *E. postvittana,* was accurately confirmed by collecting and rearing life stages of the host.

2.4.3 Interactions Between Species of Natural Enemies

Determining potential natural enemies of *E. postvittana* becomes difficult when specific interactions among species are considered. In some horticultural crops spiders significantly contribute to controlling various pests (e.g. Whitehouse and Lawrence 2001). Although considered generalist predators, some spiders may prefer specific prey, and these may include other natural enemies if and when they are available. For example, *Iridomyrmex* sp. are the preferred food of some spiders, for example members of the family Zodariidae (Greenslade and Halliday 1983). Mimetids, such as *Mimetus notius,* have been shown to be araneophagic after analysis of their diet showed that over 70% of their food consisted of other spiders (Kloock 2001). These examples not only show how important identification to species level is, but also how the specific biology of a species may influence its potential as a controlling agent.

One of the advantages of a general arthropod survey is that it can help identify groups or specific taxa that warrant further investigation to help address specific questions (New 1996). There were many potential predators identified from this survey. However, a deeper understanding of individual predatory and parasitic species was clearly needed in order to determine whether they make a significant contribution to suppressing numbers of *E. postvittana*. The results from this part of the study were used to guide subsequent research which focused on hymenopteran parasitoids, particularly *D. tasmanica* and the predatory mite *A. baccarum.*

CHAPTER 3

Seasonal Abundance of *Epiphyas postvittana* Larvae and Parasitism by *Dolichogenidea tasmanica*

3.1 INTRODUCTION

Epiphyas postvittana is regarded as the most important insect pest in vineyards in southern, South Australia. Anecdotal information from local growers indicates that this pest causes most damage to certain grape varieties, especially Chardonnay. Until this study, no research had been undertaken to explore this claim.

There had been a number of species of arthropod that have been recorded preying on and parasitising eggs and larvae of *E. postvittana*. However, most of this information has been the result of incidental observations while conducting research on the biology and behaviour of *E. postvittana* and has been recorded from regions other than the Coonawarra and from crops other than grapes (Nicholls 1934, MacLellan 1973, Cordingley and Danthanarayana 1976, Farrugia 1976, Buchanan 1977, Danthanarayana et al. 1977, Danthanarayana 1980a, b, Farrugia 1981, Baker and Lang 1983, Baker 1983, Buchanan and Amos 1988, Baker and Bailey 1993, Glenn et al. 1997, Thomson et al. 2003). It is clear from these studies that egg parasitoids, primarily trichogrammatids (Glenn et al.1997) and larval parasitoids, such as *D. tasmanica*, may contribute to suppressing populations of *E. postvittana* (Danthanarayana et al. 1977, Danthanarayana 1980b, Glenn et al. 1997). However, there are several additional larval parasitoids of *E. postvittana* found in the Coonawarra than have previously been recognized (see Chapter 2, section 2.3.3.4 and Appendix 2), and it is unclear what, if any, role they play in reducing numbers of *E. postvittana* in vineyards.

This chapter examines the relative abundance of *E. postvittana* larvae and levels of parasitism experienced by this host for three consecutive seasons 2002 to 2005, in Chardonnay, and for one season (2004-05) in Cabernet Sauvignon. This chapter also provides the basis for experimental work presented in Chapters 4 and 6.

3.2 MATERIALS AND METHODS

3.2.1 Sites

Broad acre crops dominate land use practices surrounding the Coonawarra grape-growing region. These crops include pea, broad bean, canola and clover, that have all been recorded as hosts of *E. postvittana*. Land use to the south and east of the region is dominated by grazing pasture. There are also large tracts of plantation eucalypt and pines (*Pinus radiata*) approximately 15 km to the east and west. In addition, there are several isolated areas of native vegetation in the region. The largest is 541 ha adjacent to the north-eastern tip of the Coonawarra grape-growing area.

The three sites used in the study, Kidman, Messenger and Provis, are described in detail in section 2.2.1. They were similar in rootstock variety, age, soil and trellising. However, they differed in the way in which *E. postvittana* was managed. Both the Kidman and Messenger sites used a pest management strategy typical for most vineyards across the Coonawarra region. However pest management at the third site, Provis, differed in using only Bt insecticides, and fungicides less frequently, compared to the other two sites.

The surrounding land use for each of the three sites was also different. The Provis site was bordered by 80 ha of native vegetation (east), *Pinus radiata* forest (north) and intensive potato and onion horticulture (north-west). The Kidman site was surrounded more or less by contiguous vineyards punctuated with areas of gum-studded grazing pasture. The Messenger site was surrounded completely by vineyards.

3.2.2 Data Collection

Epiphyas postvittana larvae were collected from grape vines for three seasons 2002-05. All larvae were placed in individual plastic cups with grape vine leaves in the insectary and reared at 25º C L/D14:10. The development of larvae was monitored until pupation or death occurred or parasitoids emerged.

3.2.2.1 Parasitism - First Season 2002-03

During the biodiversity survey (Chapter 2) conducted in 2002–03, 30 min timed searches of Chardonnay vines were conducted once a month at the Kidman, Messenger and Provis sites. All stages of *E. postvittana* found were collected, location details recorded, and individuals placed in separate plastic cups with grape vine leaves.

3.2.2.2. Parasitism - Second Season 2003-04

Parasitoid rearing was continued into the second year, 2003-04, then experiments were conducted to determine if larval parasitoids of *E. postvittana* displayed density dependent parasitism at the Kidman and Messenger sites. The experiment involved removing the naturally occurring larvae and returning them to the laboratory to rear out any parasitoids to determine rates of parasitism at larval densities occurring in the field. Then 'clean' vines were inoculated with laboratory-reared individuals of known ages at varying larval densities. Grape vine panels consisted of vines between two trellis posts; trellis posts were evenly spaced at 6 m throughout the vineyard, and rows were 3 m apart at each site. Twenty randomly chosen panels, consisting of three vines only, were used at each site, and the experiment was repeated three times between November 2003 and February 2004. Prior to adding the experimental *E. postvittana* larvae, referred to as the 'inoculation population', each experimental unit, (i.e. panel) was searched and the larvae that occurred naturally were collected and removed. Individual larva were placed in a 70 ml plastic cup with vine leaves; these larvae were referred to as the 'natural population'. Ten days after adding the 'inoculation population' vine panels were searched and larvae were recovered. The information from naturally occurring *E. postvittana* larval densities, species of larval parasitoids, and parasitism are presented in this chapter. For disease control both sites used a number of chemicals. For the control of *E. postvittana* both sites used Dipel® and Avatar®. Avatar® was sprayed 10-12 days before the second inoculation date/experiment at both the Kidman and Messenger sites on 19 and 17 December 2003, respectively. Dipel® was used at both sites but was not sprayed on experimental vines except at Messengers when it was used 24 h prior to the second inoculation experiment on 7 January 2004.

3.2.2.3 Parasitism - Third Season 2004-05

In the third year, 2004-05, the density dependent parasitism experiments were repeated, but using naturally occurring *E. postvittana* populations of varying densities in Chardonnay and Cabernet Sauvignon at all three sites. Only the data on *E. postvittana* larval density, species of parasitoids, and parasitism levels are presented in this chapter (see Chapter 4 for parasitoid response to host density). Six panels of each of two varieties, Chardonnay and Cabernet Sauvignon, were chosen randomly at each site every fortnight for 16 weeks (a total of 8 periods) between 23/10/2004 and 23/1/2005, and no panel was used more than once. Data from 23/10/2004 and 6/11/2004 at the Kidman site for Cabernet Sauvignon were not collected and not completed for 19/11/2004 due to unavoidable logistical problems and bad weather. The panels were searched carefully and all life stages of *E. postvittana* were collected and reared as mentioned above. For the control of *E. postvittana* all three sites used Dipel®, however Kidman and Messenger sites also used Avatar®. At the Kidman site Dipel® was

sprayed between experimental dates 1 (23/10/04) and 2 (6/11/04), and 2 and 3 (19/11/04) on 28/10/2004 and 16/11/2004. Avatar® was sprayed at Kidmans between dates 4 (3/12/2004) and 5 (17/12/04) on 9/12/2004 and at Messengers prior to experimental date 4 (3/12/2004) on 1/12/2004. Dipel® was used at Messengers prior to date 3, on 9/11/2004 and after date 7 (9/1/2005), 10/1/2005. Dipel® was used at the Provis site prior to dates 3 and 4.

3.3 RESULTS

3.3.1 Abundance of *Epiphyas postvittana*

The abundance of *E. postvittana* larvae was very low in 2002-03 (Figure 3.1). The maximum number of larvae found was ten individuals collected at the Provis site early in November. Although vineyards were sprayed throughout this period, unfortunately spray data for specific sites was unavailable. The other two sites, Kidman and Messenger, did not exceed more than three larvae at any one time for the same period. In total 10.5 h was spent searching, once a month from September to March, and only 34 larvae were recovered.

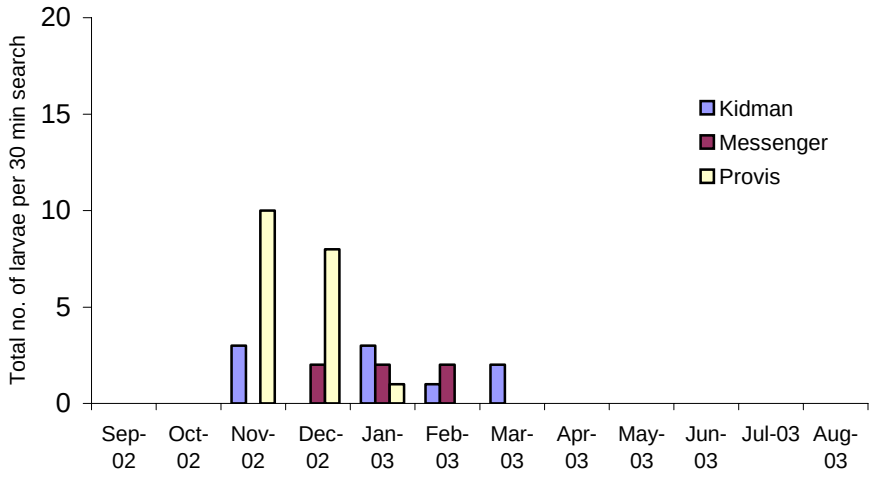


Figure 3-1 Total number of *E. postvittana* larvae collected from Chardonnay vines during 2002-2003 after searching each month for 30 min at each site (Sept 02-Aug 03).

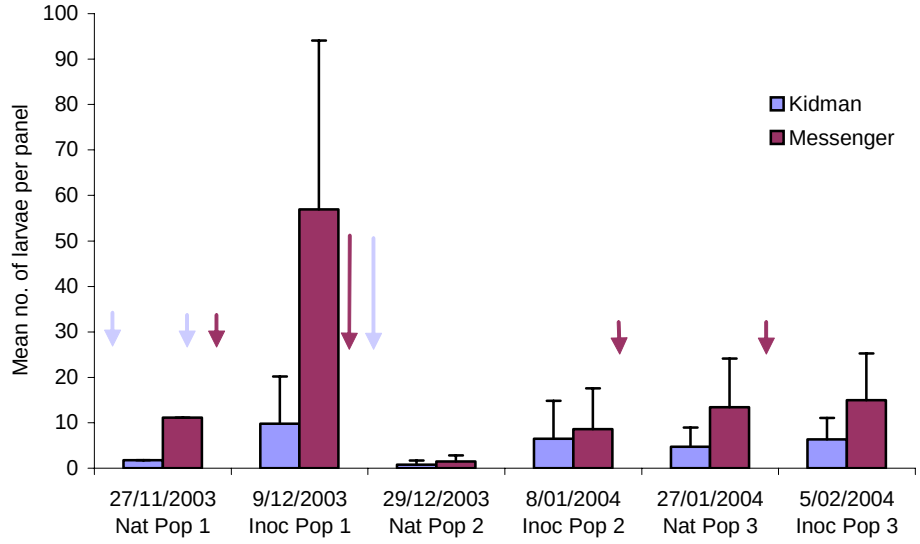


Figure 3-2 Mean number (± SD) of *E. postvittana* larvae recovered per panel in 2003-04, from Chardonnay vines. Nat Pop = naturally occurring larvae and Inoc Pop = inoculated population i.e. vines inoculated with laboratory reared larvae. Different coloured arrows relate to site. Short arrows represent the dates when the insecticide Dipel® was sprayed on vines; long arrows represent the date when the insecticide Avatar® was sprayed on vines at each site.

In 2003-04 larval density was much higher compared to 2002-03 and peaked at both Kidman and Messenger sites early in December (Figure 3.2). The maximum mean number (± SD) of larvae at Messenger was 57.0 (± 37.2), and at Kidman was five times less, 9.8 (± 10.4). The lowest mean number of larvae was recorded at the Messenger and Kidman sites two weeks after the peak, 1.5 (± 1.4) and 0.8 (± 0 .9), respectively. It is likely that this was due to, or heavily influenced by, spraying of Avatar® insecticide.

In general, in 2004-05, for every collection period at the three sites, the mean number of larvae from Chardonnay was more than five times greater than the mean number collected from Cabernet Sauvignon (Figures 3.3a,b). The maximum mean number of larvae for both Chardonnay and Cabernet Sauvignon at the Kidman site was 39.0 (± 29.7) and 15.5 (± 24.5), respectively, and at the Messenger site was 196 .7 (± 76.4) and 49.7 (± 21.2), respectively. These occurred in mid-November, three weeks earlier than the peak in 2003-04 (Figure 3.2). At the Provis site the maximum mean number of larvae collected from Chardonnay vines peaked almost two weeks later, 25.8 (± 13.6), and four weeks later for Cabernet Sauvignon, 8.8 (± 3.6).

There were also differences in larval densities among seasons. The mean number of larvae per panel for both Kidman and Messenger in 2004-05 was four times greater than the peak in 2003-04. In the 2004-05 season, the maximum mean number of larvae at Messenger was four times greater than the maximum mean for the Kidman site, and five times greater than the maximum mean at the Provis site for the same collection period. The number of larvae in Cabernet Sauvignon vines from all sites varied substantially (Figure 3.3b). The maximum number of larvae in Cabernet Sauvignon vines at Messenger coincided with the peak in Chardonnay vines in mid-november. The maximum for Kidman and Provis Cabernet Sauvignon was reached two and four weeks later, respectively. The minimum mean number of larvae for the Messenger and Kidman sites occurred four weeks after the peak and the application of Avatar® insecticide. Overall, the Provis site had consistently lower mean larval densities and less variation per panel over time for both grape varieties, than the Kidman and Messenger sites (Figure 3.3a). Also, although there is a large amount of season-to-season variation in larval density they follow a similar seasonal phenology. The density of larvae increased from the beginning of the season, peaking sometime in November or early December, and then numbers declined substantially and began to increase slightly towards the end of January.

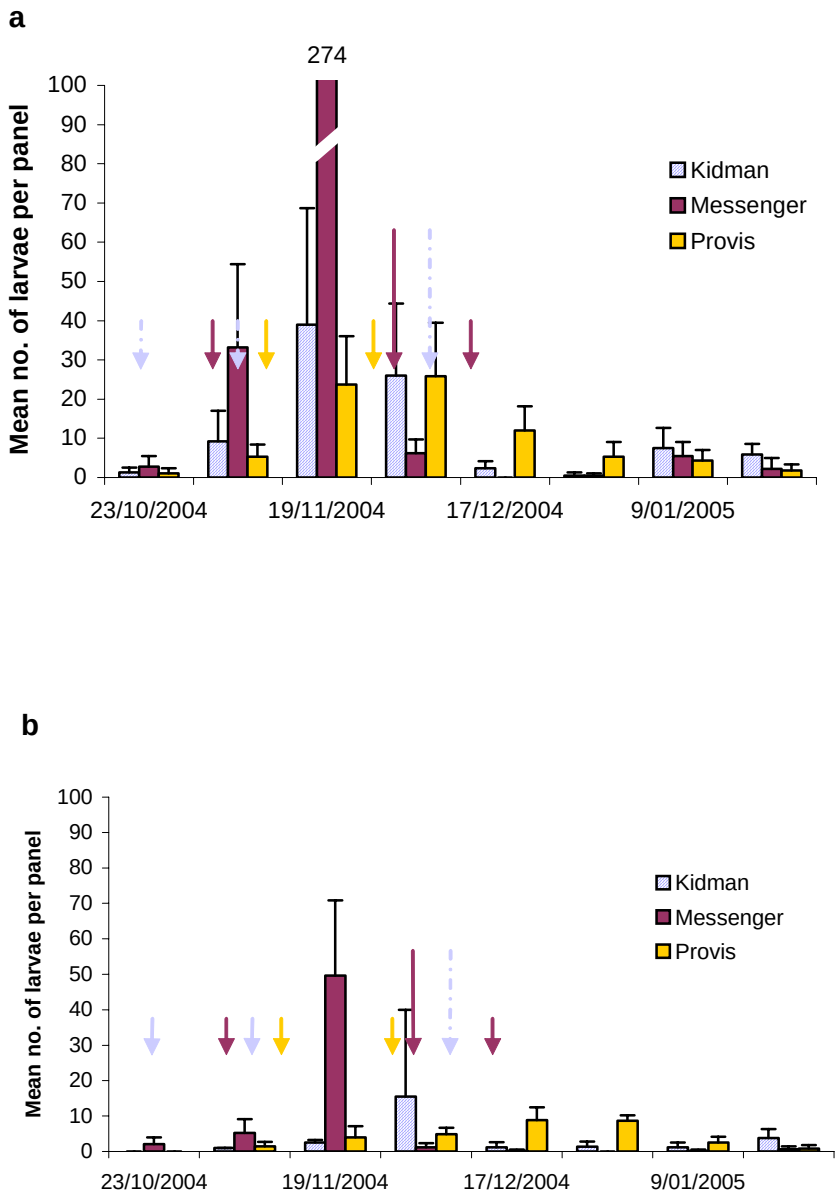


Figure 3-3 Mean (± SD) number of *E. postvittana* larvae per panel in 2004-05, collected from **(a)** Chardonnay and **(b)** Cabernet Sauvignon vines. Short arrows represent the dates when the insecticide Dipel® was sprayed on vines; long arrows represent the date when the insecticide Avatar® was sprayed on vines.

3.3.2 Parasitism

Dolichogenidea tasmanica was responsible for most of the parasitism at all sites and contributed >80% in 2002-03 and almost 70% in the 2003-04 and 2004-05 seasons (Table 3.1). Other species contributed less than 16.5% and most were responsible for less than 5% parasitism.

Table 3-1 Percentage parasitism of *E. postvittana* larvae by parasitoid species for each season pooled across sites. K = Kidman, M = Messenger and P = Provis sites. The number in brackets is the total number of individuals reared from larvae.

Parasitoid Species	Site	2002-03	2003-04	2004-05
Braconidae				
Dolichogenidea tasmanica	K, M, P	84.2 (16)	69.9 (321)	69.1 (414)
Ichnuemonidae				
Temelucha minuta	K, M, P		8.9 (41)	16.5 (99)
Eriborus postvittana	K, M, P		12.9 (59)	0.7 (4)
Chalcidoidea				
Brachymeria sp.#1	M, P			0.3 (2)
Brachymeria sp.# 2	K, M, P	10.5 (2)	0.4 (2)	3.0 (18)
Plectochorus sp.	P			0.5 (3)
Australoglypta latrobei	P			0.5 (3)
Bethylidae				
Goniozus sp.	P			0.3 (2)
Netelia sp.	P			0.2 (1)
Euceros sp.	K		0.2 (1)	
Perilampidae sp.	P		0.2 (1)	0.3 (2)
Elasmus sp.	P			1.2 (7)
Tachinidae				
Voriella uniseta	K, M, P	5.2 (1)	7.6 (35)	7.3 (44)

In 2002-03 only 34 larvae were collected from Chardonnay vines, however the majority were parasitised (Figure 3.4). Given that *D. tasmanica* was the most dominant parasitoid and was responsible for 100% parasitism six out of the 10 times larvae were collected, it is likely that it may be effective at parasitising *E. postvittana* larvae when densities are low.

In general, maximum parasitism by *D. tasmanica* in each season occured four weeks after peak larval densities (Figure 3.2), as shown in 2003–04 for both the Kidman and Messenger sites (Figure 3.5).

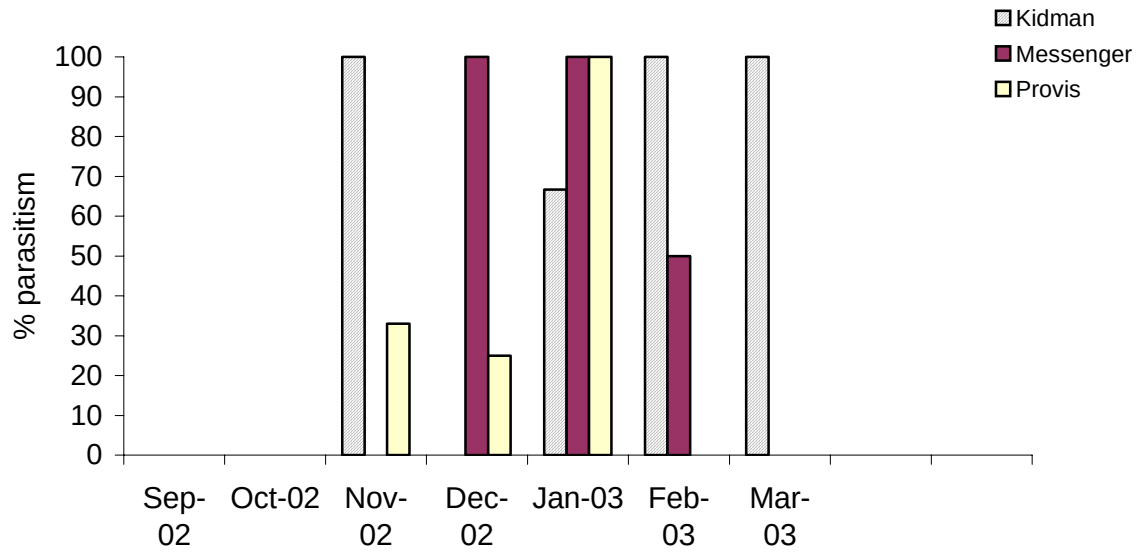


Figure 3-4 Percentage of *E. postvittana* larvae parasitised by *D. tasmanica* in Chardonnay for each sample at each site for 2002-03.

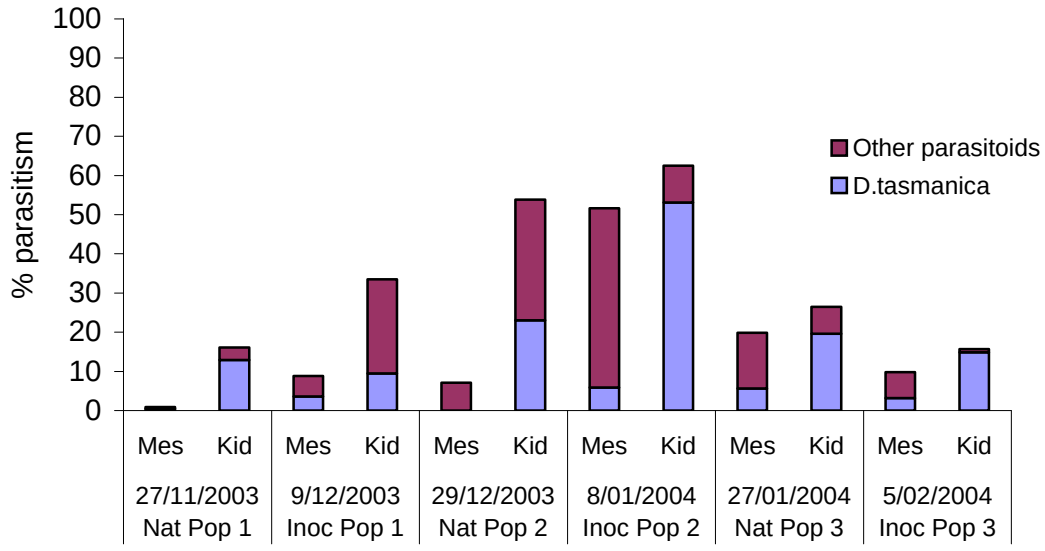


Figure 3-5 Percentage of *E. postvittana* larvae parasitised by *D. tasmanica* and other parasitoids (combined) collected from Chardonnay vines in 2003–04 at Kidman and Messenger sites.

In 2004-05 the highest parasitism by *D. tasmanica* also occurred four weeks after peak larval densities in Chardonnay and Cabernet Sauvignon at Kidman, 50% and 67%, respectively (Figure 3.6a), and Provis, 52% and 67%, respectively (Figure 3.6c). Even though the maximum mean number of larvae occurred early in 2003-04, the highest parasitism by *D. tasmanica* in Chardonnay also peaked four weeks after the maximum mean number of larvae. The exception was at Messengers in 2004-05 where the highest parasitism for Chardonnay (13%) and Cabernet Sauvignon (100%) was reached some eight weeks after peak larval density.

Parasitism by *D. tasmanica* at all three sites during 2004-05 (Figure 3.6 a-c) was higher in Cabernet Sauvignon compared with Chardonnay. For example, at the Kidman site, parasitism was higher in Cabernet Sauvignon than Chardonnay for four out of five sampling periods (Figure 3.6a), while at the Provis site, parasitism was higher in Cabernet Sauvignon than in Chardonnay five out of seven times (Figure 3.6c). Despite the extreme variability in parasitism throughout the season at Messenger, parasitism was higher five out of eight times in Cabernet Sauvignon compared with Chardonnay (Figure 3.6b). Parasitism at the Provis site was consistent through time and across varieties, with *D. tasmanica* and other parasitoids being represented in both varieties at all sampling times (Figure 3.6c). At this site, the lowest percent parasitism was 24%, but exceeded 40% for 11 sampling times, with the highest being 100%.

Interestingly, the 2004-05 season also showed the highest parasitoid species richness with 13 species present in vines versus seven species in 2003-04 and three in 2002-03 (Table 3.1). Five parasitoid species, *D. tasmanica*, *Temelucha minuta*, *Eriborus postvittana*, *Brachymeria* sp. #2 and *Voriella uniseta*, were present at all three sites, while Provis, had the highest species richness (12 spp.), with all taxa present except *Euceros* sp. (Table 3.1).

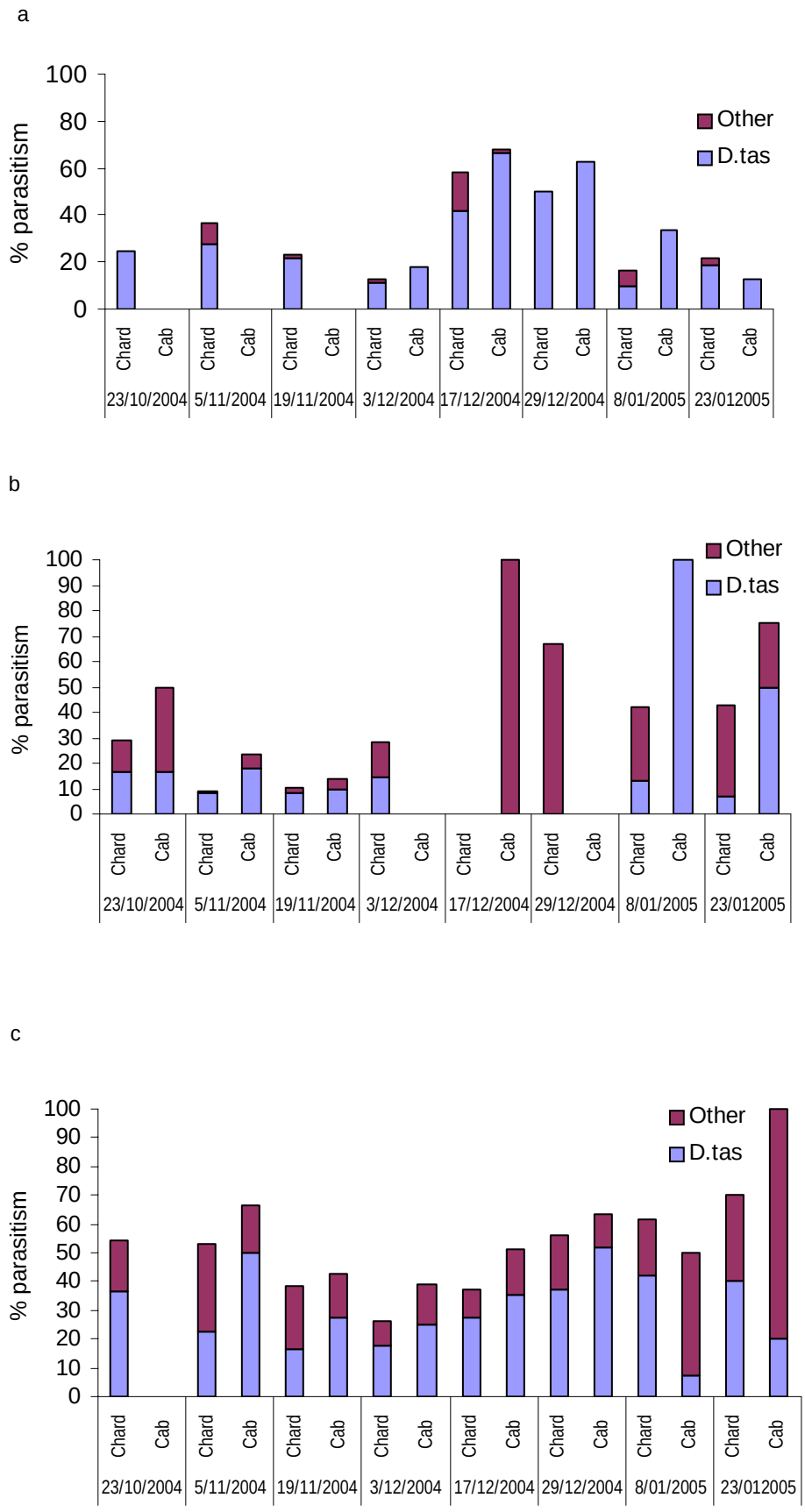


Figure 3-6 Percentage parasitism of *E. postvittana* by *D. tasmanica* and other parasitoids combined collected monthly in 2004-05 in Chardonnay (Chard) and Cabernet Sauvignon (Cab) varieties at sites **(a)** Kidman, **(b)** Messenger, and **(c)** Provis.

3.4 DISCUSSION

The results from this study clearly show that there is a large amount of variation in *E. postvittana* larval density, species of parasitoids present, and levels of parasitism among seasons, grape varieties and locations. There are a number of factors which are likely to contribute to this variation and influence oviposition and larval survival of *E. postvittana*, including climate, non-grape host plant availability, seasonal synchrony, varietal differences, vineyard management (physical and chemical), parasitoid dynamics and, host and parasitoid synchrony. These factors are discussed below.

3.4.1 Abundance of *Epiphyas postvittana*

3.4.1.1 Seasonal Variation

The number of larvae fluctuated between seasons with extremely low densities in 2002-03 and extremely high densities in 2004-05. Previous research conducted on *E. postvittana* over consecutive seasons in grapes (Buchanan 1977, Baker and Lang 1983, Baker and Bailey 1993) and apples (MacLellan 1973, Danthanarayana 1975) show a similar degree of seasonal variation in *E. postvittana* density.

According to unpublished records kept by the Coonawarra Grape Growers Association, the 2002-03 season was the 10th consecutive year of below average rainfall. Therefore, it is possible that these prolonged dry conditions contributed to the low numbers of larvae in the first season of the project by reducing the number of adults migrating into the vines. This may have been a result of low densities of adults in surrounding drought-affected crops and non-crop habitat. The subsequent seasons had higher rainfall, which may have influenced *E. postvittana* populations in surrounding crops and non-crops, resulting in an increase of migrants into vines the following season. In support of this Danthanarayana (1975) credits a drought as decimating the *E. postvittana* population in the summer of 1972-73 at Bundoora, (Victoria).

3.4.1.2 Non-Grape Host Plant Availability and Seasonal Synchrony

The polyphagous nature of *E. postvittana* means that there are many potential host plants that are available throughout the year that could sustain larvae during winter and spring when grapevines are dormant or initiating growth. In years when winter rains are less than average this would almost certainly reduce the quality and quantity of suitable, alternative host plants and, therefore, would likely reduce the *E. postvittana* populations, as observed in 2002-03. Alternatively, high rainfall years may create circumstances for larger populations of *E. postvittana* that are ready to migrate into vines as alternative host plants in the surrounding landscape senesce. *Epiphyas postvittana* larvae have been recorded from 73 host plants across

27 families, including many native plants (e.g. Danthanarayana 1975, McQuillan 1992). Common species known to occur in the Coonawarra region include evening primrose, capeweed, clovers, dock, plantago, roses, prunus, various varieties of fruit trees, and numerous native species. Many occur incidentally as volunteer weeds in vineyards, along roadsides or as ornamental plantings in the vicinity of vineyards. Most of the native vegetation in the Coonawarra is confined to isolated small areas of revegetation or larger areas as native remnants in national parks. *Pinus radiata* has also been recorded as a host for *E. postvittana* as have *Eucalyptus* spp. which are grown in plantations throughout the south-east region of South Australia.

During this study healthy larvae were found in vineyards during mid winter within dead and decaying vine leaves on the ground. Under laboratory conditions *E. postvittana* larvae also completed their lifecycle on dead grape vine foliage. Although such environments are not likely to produce large populations of *E. postvittana*, it does indicate the robust nature of the species and its ability to withstand extended periods with limited, poor quality food. A similar finding has been shown for the herbivore of English oak (*Quercus robur*) trees, the tortricid, *Tortrix viridana* (Hunter et al. 1997).

3.4.1.3 Varietal Phenology

Larval densities were also different between the two varieties, Cabernet Sauvignon and Chardonnay. Despite both varieties being adjacent to each other at each site, there were always fewer larvae in the Cabernet Sauvignon compared with the Chardonnay vines. This may have been due to moths preferring to oviposit on one variety compared to the other, larvae surviving better on one variety over the other, or differences in varietal phenology. Answering this question should be a priority in future investigations.

Records for vine phenology indicate that there is reliable synchrony in bud-burst for different varieties of grape in the Coonawarra (Coombe 1988). Chardonnay is the first variety to burst bud in about the last week of September, followed by Cabernet Sauvignon two weeks later. The early bud-burst of Chardonnay compared with Cabernet Sauvignon may explain, in part, the higher larval densities in Chardonnay. Vineyards at budburst present an extensive area of host plant in the landscape, and as moths emerge from areas of alternative host plants, or possibly from agricultural crops in the surrounding area, they are likely to exploit this reliable, seasonal and concentrated resource. Chardonnay would also represent the ‘first’ variety and an extensive area of vineyard host plants where moths could oviposit.

Synchrony between host plant and adult life stages of pests can influence populations of the latter (Hunter and Elkinton 2000). Similarly, asynchrony between host plants and location by

moths has been shown to reduce their populations, sometimes by up to 90% (Feeny 1970). Even though there seems to be little seasonal variation in bud-burst for Chardonnay, if the timing of *E. postvittana* development and adult migration varies then moths and vines will be out of synchrony in some years.

Even though it appears that Chardonnay has larger initial larval populations before Cabernet Sauvignon reaches bud-burst, moths should still be ovipositing. Therefore, a difference of only two weeks in bud-burst between the two varieties suggests that other factors may also be contributing to the difference between the two grape varieties.

3.4.1.4 Host Plant Quality

Differences between the varieties in plant and nutritional chemistry may also contribute to the higher larval densities in Chardonnay. For example, levels of phenolics in Cabernet Sauvignon are higher than in Chardonnay vines (Keller et al. 2003). There are also no epicuticular wax platelets on young Chardonnay and Cabernet Sauvignon vine leaves near the shoot tip, however, older more developed Cabernet Sauvignon leaves contain 24% more wax than older Chardonnay leaves, and exposure to ultra violet light increases not only cuticular wax, but soluble phenols (Keller et al. 2003). Further, the relative water content of Chardonnay leaves is 7% higher than Cabernet Sauvignon (Keller et al. 2003). In addition, insects require nitrogen and the dynamics of this nutrient have been postulated as the reason many insects flourish on new season growth, which is when phenolics are relatively low and nitrogen is high (Feeny 1970, Hagen 1987, Fagan 1997, Forkner et al. 2004). During bud-burst and early in the season the nitrogen concentration in vine foliage is higher than later in the season when it is reduced and tannins increase (Williams 1987, cited in (Daane and Williams 2003). Such major chemical differences between varieties therefore provide a possible reason why there were more larvae found on Chardonnay compared with Cabernet Sauvignon.

Host plant quality has been shown to influence a number of tortricid species (Danthanarayana 1975, McQuillan 1992, Torres-Vila et al. 1999, Bentancourt et al. 2003) including *E. postvittana*. Danthanarayana (1975b) showed that temperature and host plant species influenced the fecundity and pupal weight of *E. postvittana* and that these two factors varied with time, independent of host plant, providing strong evidence that there is a change in plant quality throughout the season.

The increased wax and reduction of water in the leaves of Cabernet Sauvignon vines may also influence ‘leaf toughness’ which, in turn, may make leaf roll construction more difficult, thus influencing larval survival. Vine foliage becomes tougher as the season progresses and with

this, the characteristic leaf shelters that *E. postvittana* constructed were also observed to change. Larvae exploit the curved-shape of shoots and young leaves earlier in the season, pulling the edges of leaves together using silk and constructing a classic leaf roll. As the season progressed and the amount of tender leaf material diminished, shoots abscised, and larval shelters were constructed as flat silken structures on the surface of the leaf against a leaf vein, or were formed by roughly attaching overlapping leaves together with silk. Sometimes a small part of the edge of a fully expanded leaf would be folded over flat. Previous authors have made similar observations (Danthanarayana 1975, Baker and Lang 1983). Reduction in the availability of shoots (due to shoot abscission) and suppleness of leaf tissue as the season progresses may also reduce the survival of *E. postvittana* larvae, due to increased vulnerability to desiccation or predation. This might be mediated by extended time taken to find a suitable feeding position, constructing a shelter from older less supple leaves, or change in leaf roll construction.

The differences in vine variety phenology and host plant quality are likely to influence the differences in *E. postivittana* larval density between Chardonnay and Cabernet Sauvignon. However, this does not explain why there are major differences in larval density between sites but within the same grape variety.

3.4.1.5 Site Differences

This is the first study of *E. postvittana* that has been conducted using the same crop at multiple sites within a region over a number of seasons. Despite similar trends in the abundance of *E. postvittana* across seasons and varieties, there is extreme variation in the abundance of *E. postvittana* larvae among sites. For example, for two seasons the Messenger site had five times the larval densities of the other sites.

There were differences between the sites due to physical and chemical management practices in vineyards including midrow management, canopy density and chemicals used for disease and pest management. The midrow at the Kidman site was treated with herbicide resulting in a predominantly bare midrow in the spring of 2003 and 2004. The midrow at the Messenger site was predominantly contiguous ryegrass with some volunteer broad leaf weeds such as *Plantago* sp., brassicas and *Centaurea nigra* (black knapweed), although they contributed only 3% of total cover. The midrow at Provis was replanted with strawberry clover in 2004; this died back in late December and left a sparse covering of volunteer broadleaf weeds including *Oenthera glazioviana* (evening primrose), *Marrubium vulgare* (horehound) and some brassicas. There were several alternative host plants for *E. postvittana* in low abundance at all sites except the Provis site where strawberry clover dominated at the beginning of spring.

For the control of *E. postvittana*, all three sites used Bt or Dipel®, however Kidman and Messenger sites also used Avatar®. These insecticides are designed to kill lepidopteran larvae, but Dipel® was less effective than Avatar®. After application of Dipel® larvae were still present whereas after application of Avatar® larvae were far more difficult to find. Differences in larval densities among sites were likely influenced by these chemicals, but also surrounding land use and differences in midrow management cannot be ruled out. It is likely that these factors also influence parasitoid populations.

3.4.2 Parasitoids

3.4.2.1 Parasitoid Diversity

The Provis site had the highest parasitoid diversity with more than twice the number of species as the Kidman and Messenger sites. The 'enemies hypothesis' states that increased diversity of vegetation will result in a greater abundance of natural enemies, and therefore suppress herbivore population density more in polycultures than in monocultures (Root 1973). Although some studies have found evidence contrary to this (Andow 1991, Cappuccino et al. 1998) other work has shown areas of increased plant diversity may increase or maintain natural enemy diversity because they may provide one or more benefits for parasitoids. Areas of undisturbed habitat may be required for persistent and consistent interactions (Coll and Bottrell 1996). They may also provide alternative hosts for parasitoids (Murphy et al. 1998), a range of supplementary foods and resources available all year, not just for a portion of the season (Dyer and Landis 1997), and buffer extreme climatic effects (Coll and Bottrell 1996, Dyer and Landis 1997, Torres-Vila et al. 1999, Hobbs and Cramer 2003). Therefore one of the factors contributing to the Provis site having a greater diversity of parasitoids may be its proximity to a number of different habitats, including undisturbed native vegetation. Compared to the monoculture of the vineyard, these habitats are likely to be providing a diverse range of benefits for parasitoids as indicated above.

Dolichogenidea tasmanica was the most abundant parasitoid and occurred at all sites. Very little is known about the life history of *D. tasmanica* and even less about the other species that were recorded from the study area. However, this braconid may have specific needs in order to complete its life cycle, as shown for other parasitoids (e.g. Hughes et al. 1984), and may be more resilient to disturbance as shown for the parasitoid *Hyposoter exiguae* (Miller 1980), or a better disperser (e.g. Van Nouhuys and Hanski 2002).

3.4.2.2 Differences in Parasitism

As for host density there were also differences in levels of parasitism among seasons, varieties and sites. *Dolichogenidea tasmanica* was responsible for the highest parasitism at each site. In 2002-03 there were very few *E. postvittana* in the vines, however *D. tasmanica*

was responsible on several occasions for 100% parasitism. It was also responsible for the highest parasitism at each site and for higher mortality in Cabernet Sauvignon compared with Chardonnay, even though fewer larvae occurred in the former variety. This suggests that *D. tasmanica* may be inversely density-dependent, a factor that is investigated in more detail in Chapter 4.

3.4.3 Synchrony of Host Plants

Even though bud-burst and vine phenology are relatively regular each season, any degree of asynchrony between host plant and its herbivore *E. postvittana* will affect host mortality and oviposition by parasitoids (Godfray et al. 1994, Glenn et al. 1997, Hassell 2000, Hawkins 2000, Seymour and Jones 2001). Asynchrony can be caused by climate, host plant chemistry off-setting host development, or plant phenology. For example, if *E. postvittana* larvae settle on shoots, they may be afforded greater protection against parasitism than later in the season when leaves are fully expanded. There may be an increase in larvae early in the season because dormant vines do not support *E. postvittana* or their parasitoids during winter. Therefore, it is probable that at the beginning of a season *E. postvittana* populations will increase before they are located by parasitoids such as *D. tasmanica*. There may be a time lag between production of semio-chemicals by feeding *E postvittana* larvae and the detection of these chemicals by *D. tasmanica*, and subsequent host location. This may mean that when the parasitoid arrives in the vineyard, the first generation of host larvae have developed too far and are not suitable to parasitise. These factors may account for the increase in *E. postvittana* larvae at sites in the early part of the season and be the reason parasitism almost always peaks four weeks after the peak in larval densities.

3.4.4 Varietal Differences, Location Cues

The chemical and physical differences between grape varieties are likely to influence how parasitoids locate *E. postvittana* larvae and the degree to which they can successfully parasitise them. For example, the different leaf shape and more wax of Cabernet Sauvignon foliage may mean less substantial or different leaf roll constructions, which may facilitate more effective oviposition by parasitoids. Tannin content of leaves has been shown to have a positive influence attracting some species of parasitoids. Larvae from leaves which had tannins painted on them had higher rates of parasitism compared to oak leaves without (Faeth and Bultman 1985). Cabernet Sauvignon has higher concentrations of tannins compared with Chardonnay, possibly resulting in *D. tasmanica* being arrested by specific tannin semio-chemical cues, thus resulting in higher levels of parasitism in this variety.

3.4.5 Site Differences

The major differences in parasitism levels between sites are most likely a function of colonisation by individuals from surrounding habitats, availability of refuges in adjacent undisturbed habitats, and freedom from insecticides, both as mortality to adults and by reducing the number of available hosts. An exotic horticultural crop such as grapes, despite its 'perennial framework', could be classed as ephemeral when it is compared to non-deciduous and diverse native vegetation in Australia. It has been suggested that crops like these leave de-faunated islands for part of the year that depend on non-crop habitat or winter/spring agricultural crops as sources for recolonisation (Tscharntke and Kruess 1999b).

Several studies have contributed to the idea that characteristic areas of landscape act as either sources or sinks (e.g. Pulliam 1988, Rosenheim 2001). If this is the case then these areas need to be colonised by *E. postvittana* before parasitoids are able to locate them. Successful colonisation of an area by parasitoids will then depend on the ability of an adjacent area to support a large number of natural enemies (Schellhorn et al. 1999). Patches that are isolated from sources by greater distances not only take longer to colonise but also are often characterised by lower levels of parasitism (Kruess and Tscharntke 1994). At the start of each season vineyards are more or less empty patches (sinks) isolated from areas such as perennial native habitat where *E. postvittana* and associated parasitoids may persist consistently (source).

Provis site may have had the highest parasitism due to the mosaic of different habitats around it, including large areas of native remnant vegetation adjacent to the vines which the other two sites did not have. The Messenger site had the lowest parasitism levels and this was the site surrounded by vines. It was also observed (C .Paull personal observation), that this vineyard had a reduced canopy and that this may alter the microclimate rendering vines less hospitable for parasitoids or allow better coverage and kill from insecticides.

Finally, pesticides were used more extensively at the Kidman and Messenger sites, which may explain the greater variation in larvae and parasitism among sites. However, the impact of physical disturbance to vines on numerous occasions throughout the season such as midrow slashing, shoot bashing and shoot trimming, on adult parasitoids or parasitised larvae has not been investigated yet.

3.5 CONCLUSION

The seasonal patterns and fluctuations in the populations of *E. postvittana* and associated parasitoids in Coonawarra vineyards are likely due to multiple factors. These factors take place at both the landscape and vineyard scale and include host plant quality and synchrony, phenology and chemistry. In turn, these factors also have the potential to directly influence the effectiveness or the suppression of pests by parasitoids. The results here also imply that management of the surrounding landscape, such as preserving areas of undisturbed habitat, management activities within vineyards, and the use of various chemicals also influence the populations of both host and parasitoids.

A consistent factor across seasons, sites, and varieties was the presence/activity of the parasitoid *D. tasmanica*.

The following chapters focus on specifically designed experiments to elucidate:

1. *Dolichogenidea tasmanica's* response to host density;

2. Indentification and potential implications of a multi-species interaction of natural enemies with *D. tasmanica;*

3. The role of disturbance and alternative habitats on parasitism by *D. tasmanica.*

CHAPTER 4

Response to Host Density by the Parasitoid *Dolichogenidea tasmanica* (Hymenoptera: Braconidae)

4.1 INTRODUCTION

Response to host density can indicate the effectiveness of a parasitoid as a control agent for a pest (e.g. Huffaker et al. 1976, Hawkins et al. 1994, Murdoch and Briggs 1996). For example, a parasitoid that responds to hosts in a density dependent manner, particularly when host density is low, may be able to quickly suppress pest population growth before it reaches economically damaging levels. However, there are many examples where response to host density is variable (e.g. Walde and Murdoch 1988, Cronin and Strong 1990, Connor and Cargain 1994, Hassell 2000). Possible explanations for these variable responses include issues of scale (e.g. Ray and Hastings 1996, Williams and Liebhold 2000), sampling method (e.g. Walde and Murdoch 1988), the statistical method used to test for density dependence (e.g. Holyoak 1993), lack of data from field experiments (e.g. Casas 2000), and omission of variables such as environmental parameters and host plant quality (e.g. Levins and Schultz 1996).

Searching parasitoids may respond and be attracted in greater numbers to areas with higher host density (aggregated numerical response), (e.g. Godfray et al. 1994). However, it is the combination of an individual parasitoid's functional response and a population numerical response, both aggregated and reproductive, that will influence the maximum number of hosts parasitised (Solomon 1949). There is little published information about the response of parasitoids to host density of multivoltine tortricids, but from the few studies available it appears that any trends are variable. *Mastrus ridibundus*, a parasitoid of codling moth, *Cydia pomenella*, is known to aggregate with increasing host density, but parasitism was inversely density-dependent (Bezemer and Mills 2001), while *Apanteles* sp. (Braconidae) has shown a density dependent response to increased host density of *Eudemis gyrotis* (Sugiura and Osawa 2002). The native South African egg parasitoid *Trichogrammatoidea cryptophlebiae* exhibited an inversely density-dependent response to *Cryptophlebia leucotreta* (Newton 1988), while *Goniozus jacintae* a parasitoid of *E. postvittana* showed a delayed inverse density-dependent response (Danthanarayana 1980b).

These studies, although interesting, shed little light on the nature of the response of *D. tasmanica* to *E. postvittana*. This question was therefore investigated across several vineyards by using two approaches; first by manipulating *E. postvittana* larval density on vines by inoculating them with high and low densities of even-aged individuals and, second, by using naturally occurring larval populations that varied in density.

4.2 MATERIALS AND METHODS

For both experimental approaches, the response of *D. tasmanica* to host density was only considered if at least a single host on a vine panel was parasitised. In this way it was clear that *D. tasmanica* had located the experimental hosts and, thus provided a realistic assessment of their response to host density in the area.

4.2.1 Experiment I. Inoculating Vines with *Epiphyas postvittana* Larvae

4.2.1.1 Sites

The study was conducted at the Kidman and Messenger sites at Coonawarra in South Australia (see Chapter 2.2.1 for details). These sites were approximately 1 km away from each other. Both sites were characterised by a conventional vineyard management regime (management practices that were common across the Coonawarra region), and similar in respect to age, rootstock, variety, disease management, and average shoot number. Throughout the season observable differences became apparent between the canopy and midrow management. The canopy at the Kidman site was more extensive than at the Messenger site, this was probably due to different irrigation regimes at each site. The nature of the midrows also changed throughout the course of field experiments. The Kidman site was sprayed in early summer 2003 leaving mainly bare earth with a few volunteer weeds. In contrast, the midrow at the Messenger site was predominantly ryegrass with some volunteer broad leaf weeds including *Plantago* sp., *Brassica* sp. and *Centaurea nigra* (black knapweed). Although *Plantago* sp. is a host for *E. postvittana*, it constituted less than 1% of the vineyard midrow. Dates of insecticide application for each site are provided in section 3.2.2.2.

4.2.1.2 Experimental Design and Data Collection

Ten rows of Chardonnay grape vines at each site were used for the experiment, which was repeated three times: 8-9/12/2003, 8-9/01/2004, and 5-6/02/2004. As recognised in earlier studies, collecting larvae at the scale of an individual plant proved impossible due to the interconnectedness of vine canes and cordons (Daane and Williams 2003). Therefore, 20 panels consisting of three vines only (those between two trellis posts) were randomly chosen and used as a convenient standardised experimental unit. Trellis posts were evenly spaced at 6

m throughout the vineyard; rows were evenly spaced every 2 m, and no panel was used more than once.

Prior to inoculating the vines with larvae, panels were searched to remove any naturally occurring *E. postvittana* eggs or larvae. This was done to ensure that only experimental larvae were exposed and retrieved. Each experimental unit (panel) was searched by three people for a maximum of 20 min to reduce searching bias, with searchers swapping sides after 10 min. The naturally occurring larvae were collected and transported back to the laboratory. Individuals were placed in a 70 ml cup with vine leaves, and checked every 2-3 days and development and/or parasitism recorded.

In addition, to reduce predation of inoculated larvae the vine panels were vacuumed and the vine cordons beaten using a rubber mallet to remove unwanted natural enemies. To reduce immigration of walking predators and emigration of inoculated larvae the vines were isolated by fitting plastic collars covered in tangle foot around trellis wires, posts and vine trunks. In order to gain a better fit over the irregular surface of the vine trunk, a strip of 8 mm thick, high density polyethylene foam was placed between the edge of the plastic collar and the trunk. Long trailing canes were tied into position to reduce contact points with other vines and/or the ground.

Epiphyas postvittana larvae were supplied from a culture maintained by the South Australian Research and Development Institute (SARDI). Adult moths were placed in plastic cups with a cotton wick soaked in 30% honey solution. The cups were covered with nylon gauze and kept at 23ºC. Moths were allowed to lay eggs for three days after which they were removed and then the egg cups were held at 21ºC until larvae emerged. Neonate emergence was timed to coincide with experimental dates. Grape vine leaves were added to cups for the neonate larvae to feed on while they were being transported to experimental sites.

Neonate larvae were gently tapped onto vine foliage from the rearing cups in early evening, which provided the greatest opportunity for larvae to settle before potentially hot summer daytime temperatures. Of the 20 randomly selected panels at each site, two panels were selected in each row, one high density and one low density. Host densities were artificially manipulated to create 10 panels of high (>100) and 10 panels of low (>15 but <20) larval density.

To monitor the development of the inoculated larvae and distinguish between inoculated and naturally occurring larvae, nylon sleeves were placed over three individual vine canes at each site. Twenty larvae were placed in each sleeve, which was sealed at each end for the duration

of the experiments. Ten days after larval inoculation, vines were searched and larvae were recollected. Each individual was placed in a plastic cup and maintained at 25ºC, L/D14:10 and fed grape vine leaves. All larvae were collected irrespective of age, however those that were not of the correct developmental stage were excluded from the analysis. Larval development was monitored and recorded until pupation, death or parasitoid emergence.

The data used for analysis were based on the following criteria. Over 6,000 larvae were inoculated onto vines; 2,478 were retrieved of which only 1,259 were confirmed as experimental larvae and included first, second and early third instar stages. Experimental larvae bagged on vines were used as a developmental control and indicated that neonates developed to these stages. For the analysis larvae that died (5.16%) and larvae that were parasitised by other parasitoids, (6.28%), were removed from the analysis. After this there were 1,019 experimental larvae from 101 panels. To satisfy the criteria set for the analysis, panels with no parasitism (38 panels, 559 larvae) were removed leaving a data set of 63 panels, and 560 larvae for final analysis. Of the 1,183 larvae that were not considered to be part of the experiment 30.7% were late 3rd, 27.1% were 4th, 22.8% were 5th, 5.8% were 6th instars, 11.2% were pupae and 2.4% were parasitoid cocoons.

4.2.2 Experiment II. Naturally Occurring *Epiphyas postvittana* Populations

4.2.2.1 Sites

The sites that were used in 2003-04 were also used for the 2004-05 experiment plus one additional site, the Provis site. The Provis site was 20 km NNE of the Kidman and Messenger sites, and was managed in a similar way to the other two sites but it was atypical in regard to its location, surrounding land use and pest management. The Provis site was bordered by 80 ha of native vegetation (east), *Pinus radiata* forest (north), intensive horticulture potato and onion (north-west) and grapevines (south-west). Dates of insecticide application for each site are provided in section 3.2.2.3.

4.2.2.2 Experimental Design and Data Collection

Given that there were consistently higher larval densities in Chardonnay than Cabernet Sauvignon across all three sites prior to this part of the study, these varieties were chosen and used to further investigate density-dependence (Section 3.3). Six panels of each of two varieties, Chardonnay and Cabernet Sauvignon, were chosen randomly at each site, every fortnight for 16 weeks (a total of 8 dates) between 23 October 2004 and 23 January 2005, with each panel only being used once.

Similar to experiment I, a person each side of the panel searched for *E. postvittana* larvae, uniformly working down the panel. When a larva was found the location (shoot or panel), row and panel number was recorded. Shoots consisted of the first five leaves at the growing tip of the terminal ends of individual canes. The shoot or leaf on which the larvae resided was picked and placed into an individual container along with its recorded location details. In order to counter any searching bias, searchers swapped sides of the vine panel to check for any larvae that may have been over-looked. The panels were searched carefully and all life stages of *E. postvittana* were collected and reared, as previously described.

The data for analysis were based on the developmental stage of *E. postvittana* larvae and supported by the following information. Previous research had inferred that *D. tasmanica* parasitises first and second instar larvae (Danthanarayana 1983, Berndt and Wratten 2005). There is no published information to indicate that *D. tasmanica* is able to, or does, parasitise older larvae. Therefore, subsequent analyses only focused on the larval stages that were believed to be most susceptible to parasitism; the first two instars and young third instars. Fourth instar larva and older were not included. This also meant that the results could be compared to the results of experiment I.

4.3 DATA ANALYSIS

4.3.1 Experiment I and Experiment II

The design of the experiments and the fact that *D. tasmanica* contributed 70% of total parasitism in the 2003-04 and 2004-05 seasons (Chapter 3) meant multivariate statistics, specifically logistic regression could be used to investigate the relationship between variables (see below, Tables 4.1 and 4.2), including host density as a predictor of parasitism. If no larval parasitism was recorded from a panel it was excluded from the analysis because it could not be assumed that a parasitoid located the larva. The dependant variable, parasitism, was dichotomous at two levels, parasitised and not parasitised. The progression of data analysis was guided by the protocol outlined by Tabachnick and Fidell (2001). To isolate the factors that most influenced parasitism of *E. postvittana* by *D. tasmanica*, general linear modelling (GLM) was used. GLM allows for a more versatile analysis of correlation than standard regression methods because of the function linking predictors, which are associated with the error of distribution of the dependent variable (parasitism). These can be changed depending on the characteristics of the data (Figuerola et al. 2002). The distribution of the dependent variable (parasitism) was binary, therefore a non-hierarchical binary logit link model with type three logistic regression analysis was constructed to investigate the degree to which the independent variables predicted parasitism.

Before subsequent models were run, an assessment of individual variables of the model was also made using type three analysis and analysis of parameter estimates to establish the direction of effects. Least significant predictors and interactions between predictors were removed from subsequent models until there was no significant increase in the Log Likelihood arriving at a parsimonious model. SAS statistical software was used for the analysis while SAS, PROC GENMOD were used to run the models (SAS 2000).

Converting the 'parameter estimates' (log odds) to odds ratios by exponentiation of the estimates was used to assess the strength and direction of the effect of the significant variables for the final models.

4.3.1.1 Experiment I - Inoculated Population

Larvae from high and low inoculation treatments were combined and host density was treated as a continuous variable for both the model and simple regression. Inverse logit transformations of the least square means from the model were used to determine the probability of parasitism for dates 1, 2 and 3.

4.3.1.2 Experiment II – Natural Population

Data were included from those dates where hosts were collected from both varieties. Six panels were identified as outliers and were subsequently removed. Data were then screened for multi-collinearity prior to analysis and showed no evidence of highly correlated variables, including variety and host density, even though Chardonnay was known to have higher larval densities than Cabernet Sauvignon. The following independent variables were included as predictors in logistic regression models; date, site, grape variety, stage of larvae development, the stage of leaf from which the larvae were collected (shoot or fully expanded leaf), and host density. For the initial analysis, date was used as a predictor, but it was not possible to fit a model with date as an interaction term with the other independent variables. Hence, date was included in the final model as a single variable not interacting with other variables.

Prior to analysis, results from the 'criteria for assessing goodness of fit' indicated that the deviance of the model exceeded the degrees of freedom indicating an over dispersed model. To correct for this, the data were scaled using the square root of Pearson's Chi-square (Pr Chisq) (SAS 2000). Significant results generated from models within these parameters are considered to be very conservative (Pedersen 2005).

The differences in the mean number of larvae collected from each variety for each experimental period were compared using the nonparametric Sign test (Zar 1996).

4.4 RESULTS

4.4.1.Experiment I - Inoculated Population

Percent parasitism was significantly different across dates and twice as high in January at both sites, than in December or February (Table 4.1). January parasitism was 53-60% whereas in December and February parasitism was lower at 12-30% (Figure 4.1). However, for all three dates and across sites, as *E. postvittana* density increased, parasitism by *D. tasmanica* decreased, thus indicating an inversely density-dependent response (Figure 4.2).

Table 4-1 Inoculated population analysis results

Logistic regression analysis to assess the effect of date and site on parasitism of *E. postvittana* larvae (Pr>X^2, *P*> 0.05).

Variable	Num *df*	Den *df*	F value	Pr > F	X^2	Pr > ChiSq
date	2	57	35.80	<0.0001	71.60	<0.0001
site	1	57	1.41	0.2400	1.41	0.2351
date*site	1	57	0.93	0.4000	1.86	0.3941

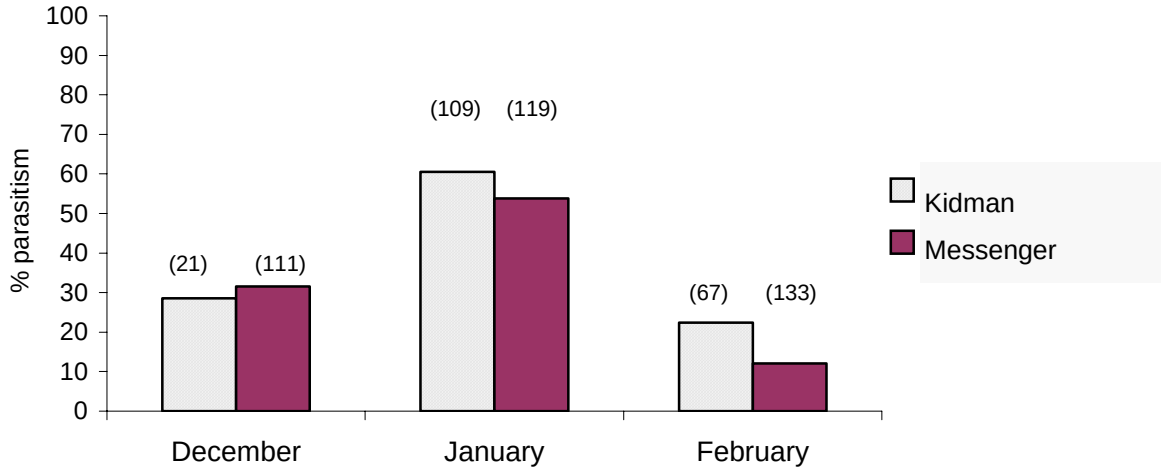


Figure 4-1 Percentage of inoculated *E. postvittana* larvae parasitised by *D. tasmanica* from Chardonnay panels for December, January and February in 2003-04 at the Kidman, and Messenger sites. Numbers in brackets are the total number of inoculated 1st and 2nd instar larvae recovered. Light coloured columns represent the Kidman site and dark coloured columns represent the Messenger site.

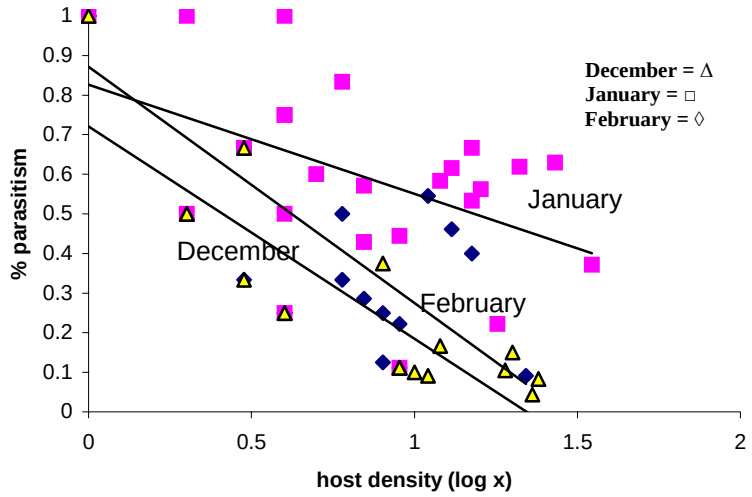


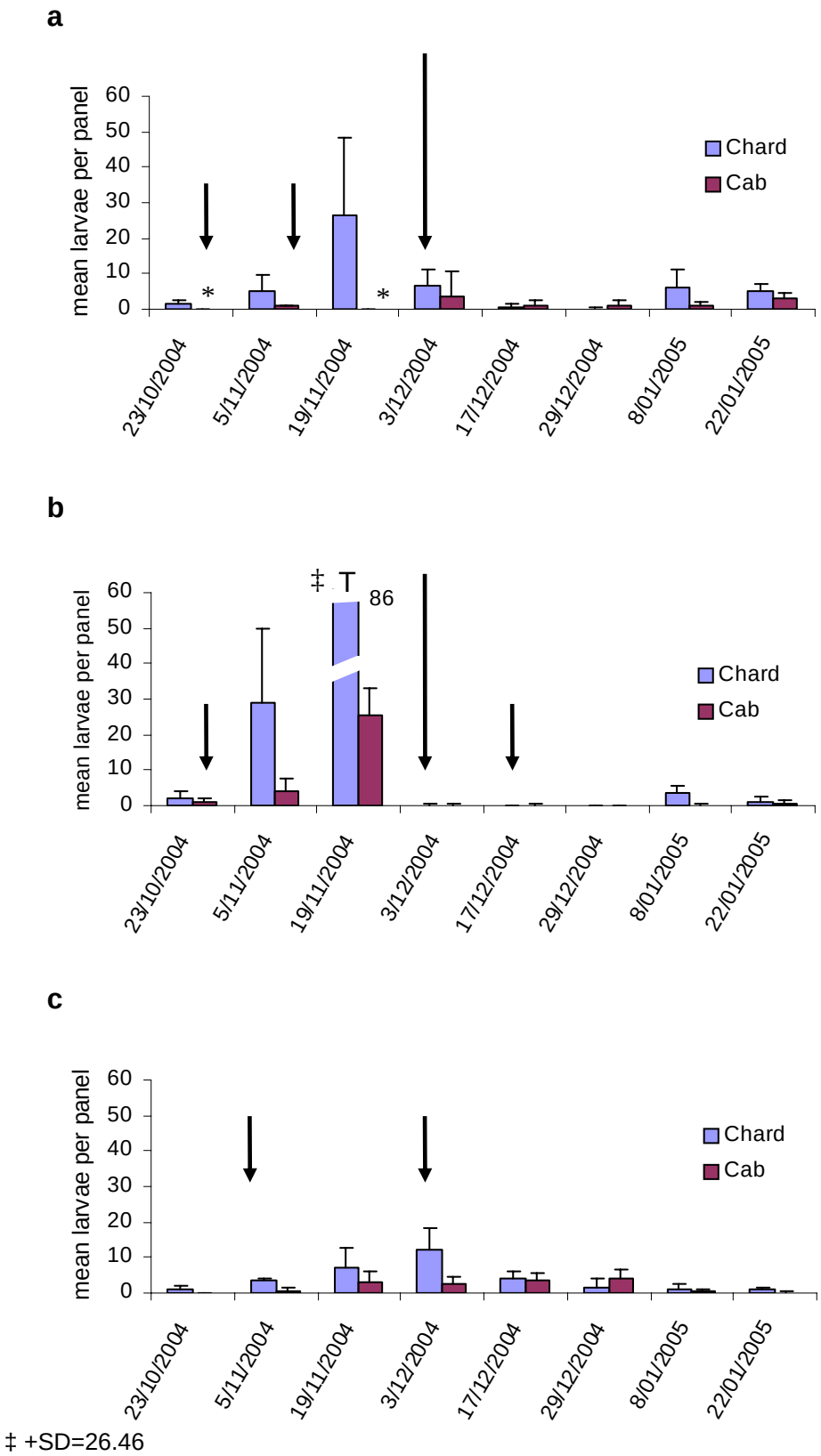
Figure 4-2 Relationship between host density and percentage parasitism by *D. tasmanica* per panel for each of the three dates during 2003-04. December y = -0.5162x + 0.7074, R^2 0.7122; January y = -0.2196x + 0.8039, R^2 0.2019; February y = -0.5907x + 0.8579, R^2 0.6286. Data from both sites were combined.

4.4.2.Experiment II – Natural Population

Eighteen of the 24 sampling dates at the three sites showed there were more early instar larvae collected from Chardonnay than in the Cabernet Sauvignon vines ($C_{0.05(6)24,}$ P = 0.05) (Figures 4.3a-c), as expected given the results in Chapter 3. Parasitism of *E. postvittana* by *D. tasmanica* was dependent on date, variety, host density, site and the interaction between host density and leaf stage (shoot or expanded leaf) (Table 4.2). Furthermore, parasitism events were less likely to take place in Chardonnay vines compared to Cabernet (Table 4.3). Similar to experiment I (inoculated larvae), as *E. postvittana* density increased, parasitism by *D. tasmanica* decreased across sites and varieties, thus showing an inversely density-dependent response (Figures 4.4a and b).

Site alone was a less significant variable influencing parasitism but showed that larvae from the Messenger site were less likely to be parasitised than larvae from either the Provis or Kidman sites (Table 4.3). The significant interaction term between leaf stage (shoot only) and the host stage indicated there was an increased likelihood of a larva being parasitised if it was in the second instar stage and found in a shoot. There was no such interaction between host stage and leaf stage (fully expanded leaves) (Table 4.3).

It was not possible to fit a logistic regression model with date (16 in total) as predictors. However, for 14 of 16 dates, as host density increased parasitism decreased. For two dates, there was no relationship between host density and parasitism.



‡ +SD=26.46

Figure 4-3 Mean (± 1 SD) number of 1st and 2nd instar *E. postvittana* larvae per panel in 2004-05 from Chardonnay and Cabernet Sauvignon varieties at sites **(a)** Kidman , **(b)** Messenger and **(c)** Provis. Chard and Cab represent Chardonnay and Cabernet Sauvignon respectively. *represents the dates where collection of larvae from Cabernet Sauvignon panels was incomplete or did not take place. The short vertical arrows represent the dates when the insecticide Dipel® was sprayed onto vines. Long vertical arrows represent the date when the insecticide Avatar® was applied to vines.

Table 4-2 Natural population analysis results

Logistic regression analysis to assess the effect of variables on parasitism of *E. postvittana* larvae Pr> X^2,*P*> 0.05.

Variable	Num d*f*	Den d*f*	F value	Pr > F	X^2	Pr > ChiSq
Date	7	120	5.01	<0.0001	35.06	<0.0001
Site	2	120	3.62	0.0296	7.25	0.0267
Variety	1	120	11.77	0.0008	11.77	0.0006
Site*Variety	2	120	1.13	0.3250	2.27	0.3216
Host Density (HD)	1	120	9.63	0.0024	9.63	0.0019
Leaf Stage (LS)	1	120	0.07	0.7852	0.07	0.7847
HD*LS	1	120	0.00	0.9608	0.00	0.9608
Host Stage (HS)	2	120	1.45	0.2375	2.91	0.2334
HD*HS	2	120	0.45	0.6365	0.91	0.6354
LS*HS	2	120	3.48	0.0341	6.95	0.0309
HD*LS*HS	2	120	1.91	0.1522	3.82	0.1477

Variable	Description
Date	Eight dates fortnightly throughout the growing season
Site	Three categories/vineyards: Kidman, Messenger and Provis
Variety	Dichotomous: Chardonnay or Cabernet Sauvignon
Host Density	Continuous: Number of larvae
Leaf Stage	Dichotomous: Larvae from shoots or fully expanded leaves on a panel
Instar	Three categories: First, second and early third instar larvae.

Table 4-3 Analysis of parameter estimates† - natural population

Variety		Site		Leaf stage "Shoot" * Host stage		Leaf stage "Fully expanded leaf" * Host stage	
	Estimate		Estimate		Estimate		Estimate
Chardonnay	-0.8731	Kidman	0 .0573	Third	-1.3806	Third	0.0000
Cabernet Sauvignon	0.0000	Messenger	-1.2203	Second	0.7743	Second	0.0000
		Provis	0.0000	First	0.0000	First	0.0000

Only significant estimates are presented (*P*> 0.05).

* Signifies an interaction term between variables.

† The estimate is represented in the form of log odds "logits". They indicate the relationship between the independent variables and the dependent variable (parasitism). A negative coefficient indicates a decrease in the likelihood of parasitism for each additional unit (larvae collected) for the given independent variable and a positive coefficient indicates an increase in likelihood and a zero coefficient is the point to which all other levels of a variable are compared. For example, larvae are less likely to be parasitised if they come from Chardonnay vines compared to Cabernet Sauvignon.

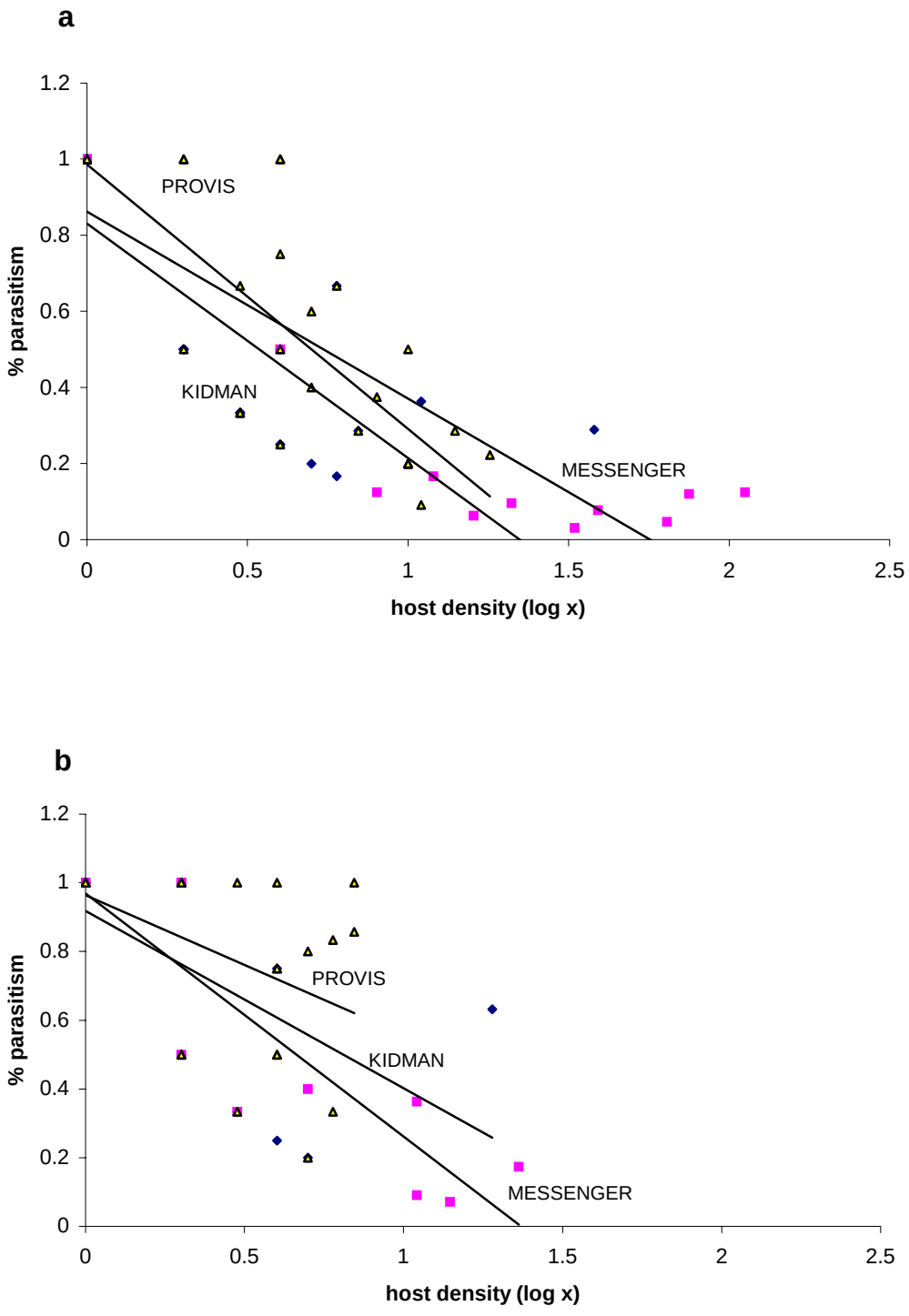


Figure 4-4 Relationship between host density per panel and percentage parasitism by *D. tasmanica* for each site by variety **(a)** Chardonnay: Kidman, y = -0.6162x + 0.8303, R^2 = 0.5993; Messenger, y = -0.4914x + 0.8618; R^2 = 0.8153; and Provis, y = -0.6944x + 0.9856; R^2 = 0.6684 and **(b)** Cabernet Sauvignon: Kidman, y = -0.5162x + 0.9183; R^2 = 0.3681; Messenger, y = -0.7078x + 0.9686, R^2 = 0.7635; and Provis, y = -0.4059x + 0.9634, R^2 = 0.2043. Data from all dates were combined and only the panels where parasitism by *D. tasmanica* was greater than zero were included. Kidman = ◊, Messenger = □ and Provis = Δ.

4.5 DISCUSSION

Response to host density by parasitoids is characterised as either density dependent, density independent or inversely density-dependent (Walde and Murdoch 1988). Results from both experiments here show that as host density increases, parasitism decreases and is therefore inversely density-dependent. In Experiment I (inoculation), as host density increased parasitism decreased at a steady rate. Also, parasitism levels varied throughout the season with date explaining the majority of the variation in the inoculation and natural population experiments. Density dependent responses can result from one of two characteristic behavioural responses from the parasitoid, i.e a functional or a numeric response (Solomon 1949, Holling 1959, Hassell and May 1986, Ray and Hastings 1996). A functional response takes place when a parasitoid kills more prey in response to increasing prey density and this is an individual behavioural response. Numerical response occurs when an increase in prey density causes an increase in the numbers of parasitoids available to attack the prey, and this is a response at the population level which may be due to increased survival, reproduction or colonisation of parasitoids (Southwood and Way 1970, Jervis et al. 2005). Although this study did not investigate the components of functional and numerical responses directly, it did investigate outcomes in terms of parasitism and host density.

Response to areas of high host density will be inversely density-dependent if the individual parasitoid or the combined functional response of a number of parasitoids is not enough to compensate for the increasing density of prey (Hassell 2000), or if there is not an aggregated population numerical response. This is supported by previous theoretical and experimental research although the specific mechanisms are not always identified or completely understood (Waage 1983, Bezemer and Mills 2001, Umbanhower et al. 2003).

The results here show date to be a significant predictor of parasitism, with over 90% of dates showing *D. tasmanica* had an inversely density-dependent response to host density. Also this inverse density-dependence does not change as the season progresses; hence there is no delayed response that might produce oscillations of parasitoids and hosts. If *D. tasmanica* was responding positively, either as aggregations of adults or as individuals ovipositing more frequently with increasing host density, one would expect an increased numerical response. Furthermore, the results of a consistent deceleration of parasitism in response to host density suggests a type 2 functional response, combined with either a zero or inverse numerical response (Holling 1959). This strongly suggests an apparent lack of aggregation and decreased survival of parasitoids. Causes of these might include limited reproduction and survival, low source populations from surrounding areas to colonise the vineyards, or limited

movement from source populations (possibly due to isolation). Each of these are discussed in more detail.

4.5.1 Reproduction and Survival

The reproduction and survival potential of some parasitoids can be enhanced by the presence of specific resources such as consumption of specific nutrients, access to carbohydrates, shelter or alternative hosts. For example, research conducted in New Zealand showed the longevity of female *D. tasmanica* supplied with water or alyssum flowers was 2.2 (± 0.17) and 15.7 (± 2.77) days, respectively under laboratory conditions (Berndt and Wratten 2005). Cumulative parasitism rates of the pest *Homalodisca coagulata* were consistently higher for vineyards planted next to prune trees, compared to the control. This was because prune trees provided an alternative host for the key parasitoid *Anagrus epos* (Hymenoptera, Mymaridae) throughout winter (Murphy et al. 1996, Murphy et al. 1998).

An inversely density-dependent response may be more likely in environments where these resources are not available or are in short supply. This is because parasitoids are likely to expend more energy and time searching for resources and, as a result, the time available to maximise their response to increasing host density is reduced (Jervis et al. 2004). This is supported by the findings from choice experiments where hungry parasitoids fed instead of ovipositing while sated wasps oviposited rather than fed (Wäckers 1994).

Management activities can also reduce the number of parasitoids available to respond to changes in host density in agroecosystems. For example, management activities such as removal of fruit infested with pest (larvae) can result in indirectly removing parasitised larvae, which reduces parasitoid numbers (Newton 1988). Chemical sprays can make carbohydrates (nectar) toxic (Cate et al. 1972) and agricultural chemicals have been demonstrated to repel parasitoids (van Driesche et al. 1998, Hodge and Longley 2000, Thomson et al. 2000). Results from this study, (Section 3.3) show that numbers of *D. tasmanica* are likely to be reduced when hosts are killed with pesticides.

4.5.2 Source Populations

Areas which support populations of parasitoids that move from suitable areas into areas that are less suitable, are referred to as refuges or source populations. Source populations are therefore important for colonisation and perpetuation of satellite populations (Pulliam 1988, Schellhorn et al. 1999, Rosenheim 2001). It has been suggested that deciduous crops leave defaunated islands when they are dormant and that they depend on non-crop habitat for recolonisation (Tscharntke and Kruess 1999a, With et al. 2002). Surrounded predominantly by other vineyards or grazing pasture, it could be argued that Coonawarra vineyards are isolated from alternative habitats such as forests, agricultural crops, and native vegetation, that may act as sources of parasitoids. Isolation has been shown to reduce the number of parasitoids that can successfully colonise or migrate (Kruess and Tscharntke 2000). The location of prune trees relative to vineyards has also been shown to influence the speed at which parasitoids could colonise vineyards at the start of the season (Murphy et al. 1998). All these factors could contribute or have a direct effect on reducing the number of parasitoids and, therefore, contribute to the resultant inversely density-dependent response.

4.5.3 Searching Behaviour

The functional response of *D. tasmanica* could also contribute to its observed inversely density-dependent response. The factors that influence a parasitoid's functional response include host location, suitability, handling time, and egg limitation (Godfray et al. 1994).

Previously, only one other study has examined a parasitoid's response to host density for more than one variety simultaneously in a field experiment. Research conducted with varieties of *Brassica* found that in the absence of hosts, parasitoids showed a significant preference for varieties but there was no significant difference in the presence of hosts. However, this work did not investigate the response to host density (Kalule and Wright 2004).

The results in the present study show that the likelihood of parasitism was greater in Cabernet Sauvignon vines compared to Chardonnay. Cabernet Sauvignon is known to contain more tannin than Chardonnay vines and increasing tannin has been shown to increase parasitism (Faeth and Bultman 1985). The consistently low density of larvae in Cabernet Sauvignon throughout the season and the possible attractive nature of increased tannin content may therefore be responsible for attracting more parasitoids.

Semiochemical cues from host insects and plants, including tannins, may also enable parasitoids to assess host suitability. Cues increase, adding complexity and noise throughout the season. As the host population grows this is likely to increase the time it takes a parasitoid

to recognise suitable hosts (Waage 1983, Casas 2000). These cues, tannins, combined with host feeding or leaf shelters, may help parasitoids locate hosts.

Early in the season, shoots are present and early instar larvae roll and web these young leaves to make their shelters. *Dolichogenidea tasmanica* may use the visual and olfactory cues of these shelters to locate hosts and parasitise the resident larvae. Therefore, a likely explanation for the interaction between shoots and 1st and 2nd instars is that shelters are more easily located by *D. tasmanica* as they stand out in the large complex mass of canopy foliage, resulting in less foliage to search. As the season progresses, shoots abscise and the volume of foliage of vines increases. This seasonal phenology could increase the inversely density-dependent response of *D. tasmanica* if the number of parasitoids emerging or colonising vineyards are not enough to offset the increase in time it takes to search vines due to an increase in foliage and hosts. This has been suggested as contributing to the differences between host density responses of *Microplitis croceipes* and *Cardiochile nigriceps* (Hymenoptera: Braconidae) under laboratory conditions compared with field experiments (Tillman 1996).

4.5.4 Host Suitability

At any one time there will always be a proportion of hosts that are unsuitable to parasitise, largely due to their developmental stage (Casas 2000). If there are a greater proportion of unsuitable hosts, the searching efficiency of *D. tasmanica* may be reduced as the parasitoid spends more time being distracted by unsuitable hosts. This is also likely to contribute to the inversely density-dependent response (Casas 1989).

4.5.5 Handling Time

Oviposition by a parasitoid takes time and can influence the functional response of parasitoids. In the case of inverse density-dependence, increased handling time leaves the parasitoid less time to find hosts and, therefore, it may not be able to capitalise on its egg load (Hassell 1982, Jones and Hassell 1988, Hassell 2000). In this study, the observed handling and oviposition time of *E. postvittana* by *D. tasmanica* under laboratory conditions was relatively short, often less than one minute and successful oviposition was frequently less than 10 sec (Chapter 5). Laboratory responses do not necessarily translate directly to the behaviour of the parasitoid in the field (O'Neil 1997), but this does suggest that searching time may be a greater constraint than handling time.

4.5.6 Egg Limitation

Hymenopteran parasitoids exhibit a diverse range of ovarian dynamics (Papaj 2000). The egg load or number of mature eggs a female parasitoid carries has been shown to directly influence the number of hosts parasitised (Heimpel and Rosenheim 1996, Heimpel and Rosenheim 1998). Modelling parasitoid population dynamics has revealed how the time required for the maturation of eggs and oviposition can contribute to inverse density-dependence by delaying the production of new parasitoids (Shea et al. 1996). Further, models have shown that the likelihood of egg limitation will increase with an increase in host encounters (Rosenheim 1996, Mangel and Heimpel 1998). Initially, research on *Cydia pomnella* showed that the parasitoid *Mastrus ridibundus* aggregated in a density dependent way, but only parasitised a limited number of larvae and may ultimately be constrained by a low egg load in combination with handling time (Bezemer and Mills 2001). This may represent maximum host utilisation for this species, which is likely to be determined by total egg load, as recognised by Waage (1983). Results from laboratory studies show that the fecundity and number of females of *D. tasmanica* can be increased by the provision of carbohydrates (Berndt and Wratten 2005). However, in what way the ovarian dynamics or reproductive potential of *D. tasmanica* is influencing results from field experiments of this study is unknown.

4.6 CONCLUSION

Parasitoids that respond to hosts in an inverse density-dependent manner are less likely to be able to control pest populations (Murdoch and Oaten 1975). Characterising the host density response of *D. tasmanica* as inversely density-dependent has helped to identify factors that are likely to compromise its effectiveness in controlling numbers of *E. postvittana.* For example, because a more or less contiguous area of deciduous vines in the Coonawarra are unsuitable for hosts and therefore colonisation by *D. tasmanica* for six months of the year, vineyards could be interpreted as isolated areas and are likely to require periodic colonisation. This, combined with frequent direct and indirect mortality from insecticides (eg. killing adult parasitoids and/or host larvae with developing parasitoids), means that parasitoid populations in Coonawarra vineyards may be constrained.

It seems likely, given the relatively short life span of *D. tasmanica* (Berndt and Wratten 2005) and the scarcity of volunteer flower resources in vineyard environments (C. Paull per observ.), that if parasitoids such as *D. tasmanica* did colonise vines they could be resource, host and subsequently time limited. Therefore, the above factors alone or in combination could result in this parasitoid being inversely density-dependent, thereby reducing the opportunity to maximise its effectiveness as a mortality agent for *E. postvittana.* In the

broadest sense, increasing the number of parasitoids in the system could help to counter most of these factors.

The results of this section of the study highlight the interaction between variety and host density which was shown to significantly influence parasitism. Although it is not clear why the proportion of hosts parasitised in Cabernet Sauvignon is consistently higher compared with Chardonnay, it is likely that differences between grape varieties, in host plant chemistry or phenology are involved. These differences may facilitate more efficient host recognition, while phenological differences in leaf and shoot structure between varieties may make larvae in Cabernet more accessible, resulting in greater parasitism. This result presents an option for changing management practices to conserve parasitoid populations. That is, by removing pesticide sprays from Cabernet Sauvignon where there is relatively low *E. postvittana* pressure but increased parasitism, it may be possible to conserve parasitoids so they recolonise areas that have been sprayed, thus contributing to reducing disruption of the 'ecosystem service' at a vineyard scale.

CHAPTER 5

Multi-Species Interactions: Wasp Parasitism Facilitates Predation of Tortricid Larvae by Predatory Mites

5.1 INTRODUCTION

The complexity inherent in ecological processes underpinning biological control means that only recently has the classic single focussed predator-prey interaction been widened to include investigating multi-species interactions (Price et al. 1980, Rosenheim et al. 1995, Idris and Grafius 1997, Rosenheim et al. 1999, Schellhorn and Andow 1999b, Cardinale et al. 2003, Fournier et al. 2003, Harmon and Andow 2003). A great number of these interactions are vaguely defined and/or poorly understood, yet some interactions have been shown to have various and important ramifications for pest suppression. Therefore, it is critical to understand the role multi-species interactions have on the population dynamics and, ultimately, the control of target organisms (Rosenheim et al. 2004).

The complex nature of multi-species interactions also makes them difficult to model and to study empirically (Sokol-Hessner and Schmitz 2002). However, modelling the likely interactions of multiple species of natural enemies has been insightful (Holt and Lawton 1994, Rosenheim et al. 1995). Some studies have predicted a negative effect on pest suppression, whereas field experiments have shown more positive effects, with examples of combined predators and parasitoids having increased pest suppression (Rosenheim et al. 1997, Tscharntke et al. 2005). Unfortunately, whether or not several natural enemies are better than one has not been resolved empirically or theoretically to date, and it is likely that this will be determined on a case-by-case basis (Holt and Lawton 1994, Murdoch and Briggs 1996, Snyder and Ives 2003).

Historically, systems with multiple predatory species were thought to interact via competition (Huffaker et al. 1984, Sih 1993). There are a range of interactions both direct and indirect that take place between predatory species and parasitoids with a range of outcomes for pest suppression (Hurd and Eisenberg 1990, Rosenheim et al. 1995). For example, a direct interaction is known for the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae) which is the host of a number of parasitoids i.e. *Cephalonomia stephanoderis*, *Prorops nasuta* and *Cephalonomia hyalinipennis*. All three species parasitise all host stages. Laboratory experiments have shown that these parasitoids exhibit interspecific competition, actively defending their hosts, resulting in a high level of parasitoid mortality (Perez-Lachaud et al. 2002). It is unclear if these interactions reduce or enhance the level of control on *H.*

hampei. A second example comes from field experiments with the coccinellid *Hippodamia convergens,* a predator of *Aphis gossypii,* where it consumed over 95 % of aphid mummies parasitised by *Lysiphlebus testaceipes*. Aphids were suppressed by the presence of multiple predators exerting a density dependent mortality to elevated numbers of aphids, despite the high level of intraguild predation. This was due to the coccinellid showing a partial preference for un-parasitised aphids (Colfer and Rosenheim 2001). Indirect interactions also occur between predators where the presence of a predator changes the behaviour of prey, making the prey vulnerable to the second predator (Losey and Denno 1998).

Interactions between multiple species of predators and parasitoids result in one of four characteristic outcomes for pest suppression; **1)** Aggregate or compensatory, when the total mortality of combined species is no greater than mortality caused by a single species (Sokol-Hessner and Schmitz 2002); **2)** Additive, when the combined mortality of several species is greater than caused by single species (Cardinale et al. 2003); **3)** Negative, when the total mortality of several predators is less than when any one predator acts alone (Rosenheim 2001, Rossi 2004); and **4)** Synergistic, when the presence of one species alters the behaviour of the prey making it more vulnerable to predation by another species (Rosenheim et al. 1995, Losey and Denno 1998). These outcomes can result from both direct and indirect interactions among natural enemies including intraguild predation (IGP) that occurs when two species of predator compete for the same prey species, but with one predator feeding on the other (Rosenheim et al. 1995, Polis et al. 2000, Muller and Brodeur 2002). This can be uni-directional where one of the interacting species acts as an intraguild predator or bi-directional (Rosenheim et al. 1995). There are examples of intraguild predation that have had negative (eg.Borer et al. 2003, Finke and Denno 2004) and positive (eg.Colfer and Rosenheim 2001) influences on pest suppression.

The results of these direct and indirect interactions for pest mortality are highly dependent on the type and behaviour of the prey. Insects have evolved numerous adaptations to defend themselves. These anti-predator strategies are evident in a number of insect groups including lepidopteran larvae (Fukui 2001, Gentry and Dyer 2002). Biting, dropping and regurgitating are direct responses used by lepidopteran larvae against attack by parasitic Hymenoptera (Gentry and Dyer 2002). Silk used in leaf rolls and ties by larvae may also offer increased protection against predation (Damman 1987). However, there has been little work undertaken to establish the interaction among multiple species of natural enemies and specific host defences.

The tortricid leaf roller *Epiphyas postvittana*, a pest of grape vines, characteristically constructs a silk shelter or hibernaculum in the form of a leaf roll or between foliage surfaces. *Dolichogenidea tasmanica* is the dominant parasitoid of *E. postvittana* in the Coonawarra region (Chapter 3). The interaction between this parasitoid and host larvae can be represented by a simple parasitoid-host model (Figure 5.1a). Observations on *D. tasmanica* and another braconid parasitoid, *Bassus* sp., has shown that when a parasitoid oviposits into larvae the host often wriggles from its shelter, potentially becoming more vulnerable to predation or parasitism. *Anystis baccarum*, is a ubiquitous predatory mite present in the grape vine canopy throughout the year (Section 2.3, Figure 2.3). Observations on *A. baccarum* in culture during this study show that, as well as being cannibalistic, they readily eat the eggs and larvae of *E. postvittana*, a behaviour also observed by Baker (1983) (Figure 5.1b). However, the silk produced by the larvae seems to preclude *A. baccarum* from entering and, in turn, preying on *E. postvittana* larvae. Hence, the aims of this part of the study were first, to determine the level of predation by *A. baccarum* on *E. postvittana* while in its silk leaf roll and when the parasitoid, *D. tasmanica* was also present and second, to determine whether *D. tasmanica* was successful at parasitising *E. postvittana* while in its leaf roll.

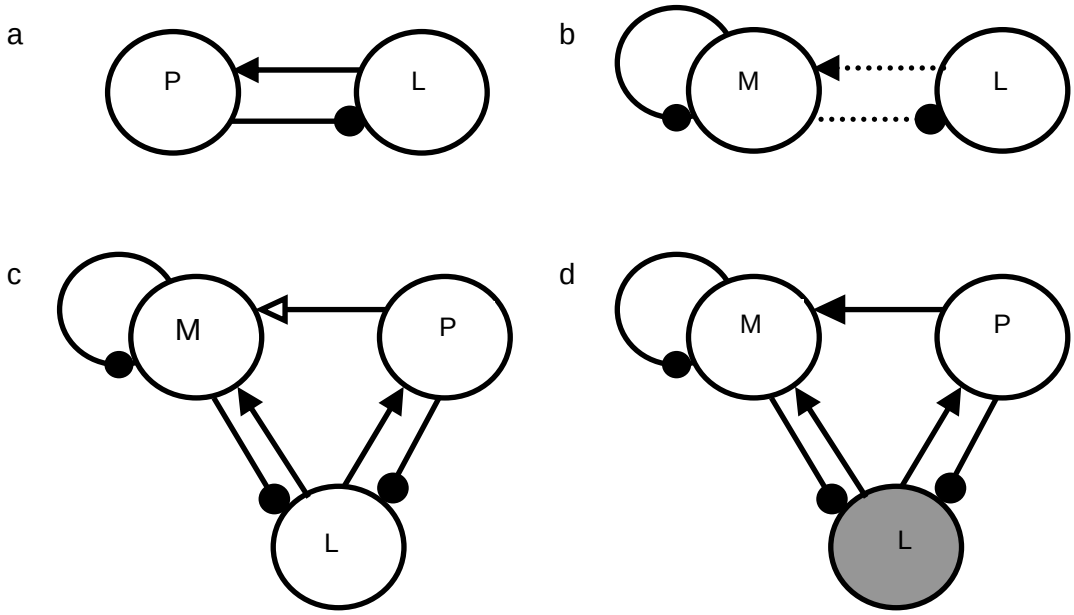


Figure 5-1 Characteristic interactions between the parasitoid *D. tasmanica* (P), predatory mite *A. baccarum* (M), and host larvae *E. postvittana* (L) after (Levins 1974, Schellhorn and Andow 1999b). **(a)** Interaction between parasitoid and host larvae; solid line with closed arrow = direct positive effect, solid line and circle = direct negative interaction. **(b)** Interaction between predatory mite and larvae; negative effect looping back to the species from which it originated = negative feedback loop, self damping due to cannibalism, broken line = weak interaction. **(c)** Synergistic interaction; open arrow = positive indirect effect. **(d)** Intraguild predation; shaded area = parasitised larvae.

5.2 MATERIALS AND METHODS

5.2.1 Rearing

Anystis baccarum was collected from sites in the Coonawarra and reared in 8 L clear plastic containers with snap on lids. A ventilation hole 6 cm² was cut into the lid and covered with fine nylon gauze. Coarsely crushed unprocessed charcoal was mixed with plaster in a ratio of 2:1 and left to set on the floor of the containers to a depth of 3 cm. This mixture, with the addition of water, helped to maintain a humid environment favourable for culturing mites. *Anystis* spp. are cannibalistic and previous rearing experience showed that the effects of cannibalism can be decreased by increasing structural complexity of the containers. The floor was purposely left to set with irregularities to increase the structural complexity of the micro-environment and two bundles of black plastic drinking straws (20 in each bundle) were added to further increase this complexity and surface area. Mites were reared on a diet of Collembola and *E. postvittana* eggs and larvae. Collembola were collected from the vineyard floor below vines and were added to containers, and thereafter provided a self-sustaining culture, presumably feeding on the moss and mould growing on the floor of the rearing containers.

To provide mites with an unlimited supply of prey, *E. postvittana* eggs and larvae were produced by releasing two female and male moths into containers once a week. Some larvae completed their life cycle under these conditions, without any host plant material. Presumably they developed on algae and mould that grew on the floor of the containers. Plastic rearing containers were kept at a constant temperature of 21º C and light regime L/D14:10. In order to stop mite cultures from drying out, the inside of the containers were sprayed with water once per week. Approximately 120 ml of water was added to the plaster charcoal mix every fortnight except in summer when water was added weekly. Additional *E. postvittana* larvae were supplied from a culture maintained at the South Australian Research and Development Institute, at the Waite Campus.

5.2.2 Loop Analysis

Qualitative modelling or loop analysis was developed by Richard Levins to help scientists represent and understand the nature of complex biological systems and help to define research questions. Loop analysis provides a systematic method of visually representing interactions between multiple species. The interactions are represented by diagrams called digraphs (directed graphs), the circles represent variables, in this case species, and lines represent the flow of energy. Interactions can either be negative, represented by a line with a solid circle at the end of it, positive, a line ended in an arrow or no effect, the absence of a line. A line extending from the variable and looping back on its self represents feedback, which can also

be negative or positive (Levins 1974). The diagrams here are used to represent the interactions between the species in the following experiments (Figure 5.1a-d).

5.2.3 Experiment I Predation, and Experiment II Parasitism

Experimental arenas for both experiments consisted of 70 ml cylindrical plastic vials sealed with a screw-on plastic lid; each lid was punctured with four small holes. Leaf discs of 3.5 cm diameter were cut from fresh Chardonnay leaves. All leaf material was washed and inspected to exclude any additional prey. Prior to the experiment the inside of the arenas were sprayed with a fine mist of water to maintain leaf quality. The leaf disc was placed in the arena so that only a small part of the leaf edge came into contact with the sides of the arena. This allowed access to both sides of the disc by the wasp and/or mite. *Dolichogenidea tasmanica* were collected from the Coonawarra and reared in culture. All female wasps were 24 h old, had access to males and had presumably mated.

5.2.3.1 Experiment I Predation: Penetration of Leaf Shelter by *A. baccarum*

Experiment I was conducted to see whether *A. baccarum* could enter the silk shelter and prey on *E. postvittana*, and determine the outcome of the interaction among *A. baccarum*, *D. tasmanica* and *E. postvittana*. Two 1st instar *E. postvittana* larvae were placed on a vine leaf disc inside each arena.

Mites are difficult to age and sex without damaging them, so they were categorised based on culturing experience, i.e. the date since emergence and approximate size. Mites were starved 24 h prior to beginning the experiment. All experiments were conducted at a temperature of 21º C and light regime of , L/D14:10.

There were four treatments, each replicated ten times with individual mites and parasitoids only being used once. Treatments consisted of, experimental arenas with: 1) two *E. postvittana* larvae plus one mite added simultaneously (no leaf disc); 2) a leaf disc, two larvae plus one mite added simultaneously; 3) a leaf disc, two larvae which had been introduced 24 h earlier to allow them to construct a silk leaf shelter, plus one mite; and, 4) a leaf disc, two larvae which had been introduced for 24 h earlier to allow them to construct a silk leaf shelter, plus one mite and one female parasitoid, with the mite and parasitoid being added simultaneously.

Effectively, treatment 1 and 2 acted as controls; treatment 1 without a leaf disc, and treatment 1 and 2 where the larvae were added at the same time as the mite so there was no time for the larvae to spin a silk shelter. After 24 h the mortality of the larvae was recorded.

5.2.3.2 Experiment II Parasitism: Vulnerability of Larvae in Leaf Shelter

To investigate how successful *D. tasmanica* was at parasitising *E. postvittana* in its leaf roll, one larva was added to an arena 24 h prior to the start of the experiment. The experiment was repeated five times for 10 individual parasitoids (n= 50). The experiment started when a parasitoid was transferred into the arena. One of two characteristic behaviours was recorded when either the ovipositor of the wasp came into contact or was inserted into the larvae (stung); 1) the larvae exited the leaf roll, or 2) the larvae remained in the leaf roll. As soon as the contact and/or oviposition event finished the parasitoid was removed from the arena. Oviposition often took less than three seconds. Individual larvae were then reared through and parasitism recorded.

5.3 DATA ANALYSIS

A Kruskal-Wallis test was applied to the data to compare percentage mortality among treatments in experiment I using JMP, Version 3.2.1 (Sall and Lehman 1996). In experiment II there was no significant difference in the proportion of larvae parasitised by naïve wasps (first oviposition) and subsequent oviposition events so the data was pooled. A *G* test for a 2x2 contingency table with a Yates correction was used to determine the relationship between parasitism and behaviour of larvae. (Zar 1996).

5.4 RESULTS

5.4.1 Experiment I Predation

There was a significant difference in the proportion of larvae killed for each treatment (X^2 = 15.28, n = 43, df = 3, $P < 0.05$). Larval mortality for treatment 1 (where no leaf roll material was available for the larva) and treatment 2 (no time was available for the larva to make its roll prior to the mite being introduced) were 63.6 and 68.2%, respectively (Figure 5.2). The lowest mortality was recorded for treatment 3, where the larva had a chance to make a leaf roll prior to the introduction of the mite (16.6 %). The highest mortality was recorded for treatment 4, where the larva made the leaf roll prior to the simultaneous introduction of the mite and parasitoid (72.2 %). However, this result was not significantly different from treatments 1 and 2.

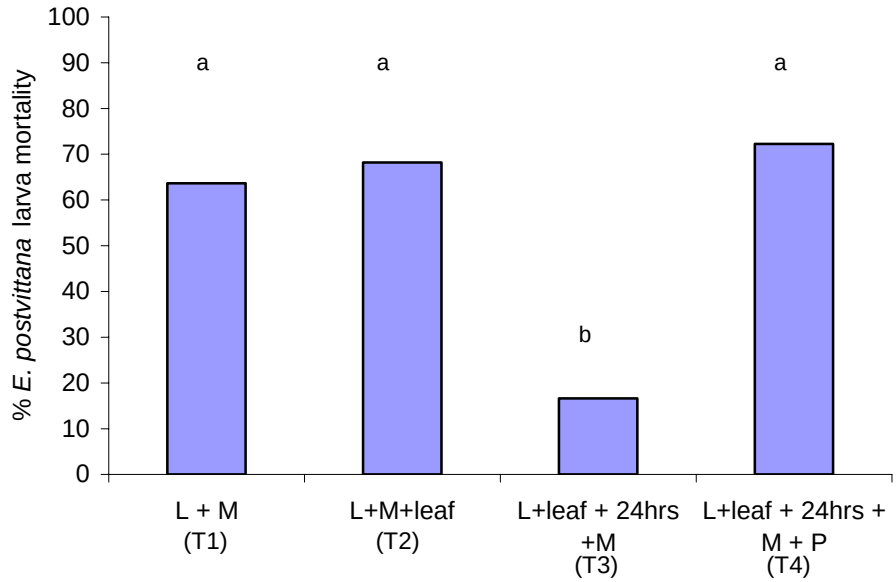


Figure 5-2 Percentage mortality of *E. postvittana* larvae for each of four treatments. L = *E. postvittana* larvae, M = predatory mite *A. baccarum* , leaf = leaf disc, 24 h = larvae exposed to leaf disc for 24 h period prior to predatory mite or predatory mite plus a parasitoid being introduced into the arena, and P = parasitoid. Treatments with different letters are significantly different from each other (Kruskal Wallis $P < 0.05$). T = treatment no. (see text).

5.4.2 Experiment II Parasitism

After *D. tasmanica* stung the larva in the leaf roll, over 65% of the larvae exited the leaf roll, and of those 15% were not parasitised and 50% were parasitised. Of the 35% of larvae that remained in the leaf roll, 2% were not parasitised and 33% were parasitised (Figure 5.3). Sucessful parasitism was independent of whether the larva remained in the shelter or exited it. (*G* Yates corrected 0.8367, *df* =1, *ns P >0.05*).

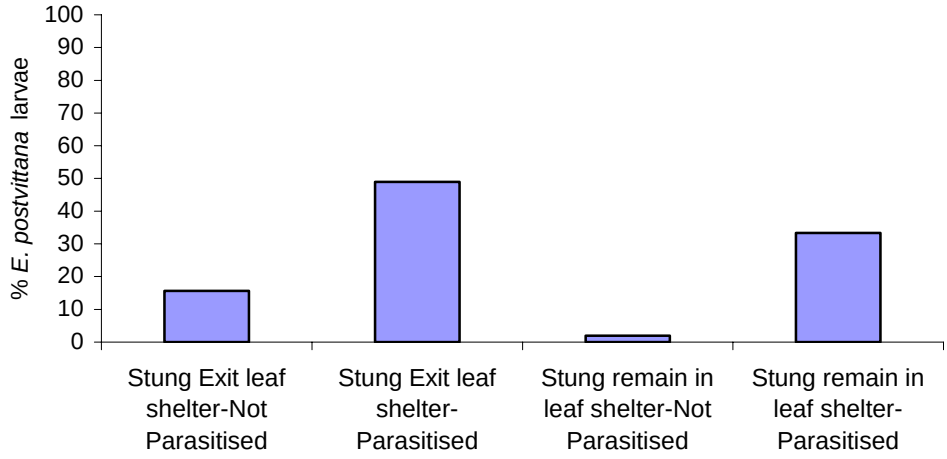


Figure 5-3 Percentage of *E. postvittana* larvae parasitised in experiment II and the immediate behavioural response after being 'stung' by *D. tasmanica*.

When considering the results of both experiments together, 50% of the interactions among *E. postvittana, A. baccarum* and *D. tasmanica* resulted in intraguild predation, the mites consuming larvae that were successfully parasitised (Figure 5.1d) and 15% of these cases were characteristically synergistic, that is the presence of the wasp altered the behaviour of the larva making it vulnerable to predation by the mite (Figure 5.1c).

5.5 DISCUSSION

In this multi-species system the interaction between the parasitoid and mite can result in synergistic pest suppression, and asymmetrical intraguild predation. Clearly the act of parasitism alters the behaviour of *E. postvittana* larvae making them more vulnerable to predation by the mite. Observations during the experiment showed that as *D. tasmanica* oviposits into *E. postvittana* the larva wriggles from and exits its shelter, leaving it vulnerable to predation by the mite. While the response of *E. postvittana* exiting its leaf shelter as a response to the parasitoid ovipositing has been recorded before (Suckling et al. 2001), this is the first experimental demonstration of how this behaviour influences a multi-species interaction resulting in an increased chance of mortality for *E. postvittana* larvae.

In the absence of the parasitoid, *A. baccarum* was unable to easily get through the silk of the leaf roll, and thus has difficulty preying on the larva within. However, *A. baccarum* is an effective predator when it could access the larva directly, and killed over 60% of those not protected in a leaf shelter. In the absence of the mite, parasitism was still high (80%), however 15% were disturbed from their leaf roll but not parasitised, and therefore potentially vulnerable to predation by the mite.

Dolichogenidea tasmanica is effective at parasitising larvae, at least under experimental conditions, with 80% successful ovipositions. Therefore, predation on parasitised larva results in asymmetrical intraguild predation. Although consumption of a parasitoid indirectly by consuming a parasitised host is not unusual (Rosenheim et al. 1995, Rosenheim 1998, Brodeur and Rosenheim 2000, Colfer and Rosenheim 2001), there is a disadvantage for a parasitoid that occurs in the same environment as a predator because it is successful oviposition that has the potential to determine the fate of the host. If parasitoid oviposition has been successful and a predator consumes the host there is a negative effect on the parasitoid population (Gentry and Dyer 2002). In this system, the presence of the mite appears to have a negative impact on the parasitoid and, although in the short term, the outcome for pest suppression seems synergistic, in the longer term as the mite population increases, they could cause greater mortality on the parasitoid, and in turn reduce mortality to *E. postvittana*. Of

course, multi-species interactions are also influenced by the species present and their synchrony in time and space, availability of alternative prey, prey abundance, and population density (Abrams 1987, Hurd and Eisenberg 1990, Brodeur and Rosenheim 2000).

5.6 CONCLUSION

Although there are numerous examples of intraguild predation, very few studies have evaluated the implications for the prey/host. In part, this is due to the complication of maintaining and managing multiple species in experimental systems. Although this study is a simple laboratory one and the results need to be verified in the field, an important mechanism involved in multiple species interactions has been identified.

The results indicate that the interaction may benefit management of *E. postvittana* in the short term, but the dynamics will fluctuate depending on the population density of the mite. For example, stronger intraguild predation would be expected when mite populations increase and, therefore, could potentially suppress parasitoid populations, hence reducing mortality to *E. postvittana*. Alternatively, in the absence of parasitoids, the contribution of the mite to mortality of *E. postvittana* is likely to be greatly reduced. This could be explored more thoroughly in future research using a model to construct a range of scenarios of differing strengths for interactions among species, different population densities, and the subsequent effects for persistence of these populations.

Understanding the impact of this interaction at a larger scale may influence the design of management strategies for pests such as *E. postvittana*. It may become prudent to monitor a combination of predators in unison and/or to develop methods to actively discourage or encourage specific predatory species to achieve the most effective control.

CHAPTER 6

Association between the Parasitoid *Dolichogenidea tasmanica* and Native Vegetation

6.1 INTRODUCTION

Disrupting trophic links within ecosystems can compromise ecosystem functions and services related to pest control (Corbett and Plant 1993, Tscharntke et al. 2002a, Wilby 2002) see also Fisher 1998 in (Hunter 2002). Evidence suggests that specialist natural enemies, such as parasitoids, are more easily disturbed and can become locally extinct when the landscape is fragmented (Thies and Tscharntke 1999, Kruess and Tscharntke 2000, Wilby 2002). This is important when crops are dependent upon surrounding habitats, native remnants and other nearby crops, to provide a source of parasitoids to colonise and suppress pests. Surrounding habitats may be a source of natural enemies because they provide shelter, hosts (alternative hosts or the key pest species), and food for adults, all of which may enhance their longevity, fecundity and survival (Landis et al. 2000). Therefore, if surrounding habitat provides a source of natural enemies that attack crop pests then, depending on their temporal and spatial relationships, it is possible that they could be managed to benefit natural enemies.

There is currently an increased focus on identifying ways to enhance the effectiveness of endemic natural enemies for conservation biological control (Murphy et al. 1996, Steinbauer et al. 2001, Chen and Welter 2002, Ovruski et al. 2004, Short and Steinbauer 2004, Grosman et al. 2005). Specifically, if the pest is a native insect, then identifying native vegetation or habitats that support the pest and its associated natural enemies may allow for an area wide, self sustaining, and long term management strategy for maintaining, restoring and/or extending such habitat in order to sustain, increase or reinitiate parasitoid populations via colonisation (Thompson et al. 2001). However, this approach has to be balanced against the notion that these same habitats are potentially providing sources of colonising pests.

Although *E. postvittana* is native to Australia there are no records of this pest causing damage to native vegetation. However, there are several native parasitoid species that attack *E. postvittana* in grape vines (Paull and Austin 2006), (Appendix 2).

The aims of this part of the study were to: 1) determine whether *D. tasmanica* occur in areas of native vegetation in the Coonawarra region of South Australia, 2) determine if there is an association between *D. tasmanica* and the level of disturbance in different areas of the region,

and 3) determine where *D. tasmanica* first occurs, at the beginning of grape growing season, in vineyards or native vegetation?

6.2 MATERIALS AND METHODS

To address these aims and determine over what distance native parasitoids are likely to have an effect, discrete patches of prey were created by placing *E. postvittana* larvae on sentinel plants (*Plantago* sp., see below) in the field. Sentinel plants have been used extensively for similar experiments on a range of insects (Weseloh 1972, Doutt and Nakata 1973, Luck et al. 1988, Gould et al. 1992, Schoenig et al. 1998, Symondson et al. 2002, Van Nouhuys and Hanski 2002, Pfannenstiel and Unruh 2003).

6.2.1 Sites

Six sites were used, each chosen to reflect a specific 'natural treatment'1) undisturbed native vegetation (two sites) 2) native re-vegetation with some disturbance, 3) undisturbed native vegetation adjacent to a vineyard with reduced chemical inputs, 4) a highly disturbed native re-vegetation site and 5) a standard vineyard site. Each site was scored based on an arbitrary assessment of the type and severity of disturbance, and level of exposure, i.e. the degree to which sentinel plants at each site were exposed to each of three broad disturbance factors (chemical, physical and climatic). Each site was alotted a score, with a maximum of three points if the disturbance factor was extreme. Points for each of the three factors were summed for each site and used to rank site disturbance (Table 6.1). A schematic view of sites is presented in Figure 6.1.

Glenroy National Park is(37º13' 990S 140º51' 665E) 3 km north-east of the Connawarra region while the Penola Conservation Park (37º12' 631S 140º41' 862E) was 15 km west-south-west of Penola. These were the two areas of undisturbed native vegetation close to Coonawarra vineyards (**Treatment 1**) (Figure 6.1). While most of the upper-storey tree species were similar for both sites and included *Eucalyptus viminalis, E. obliqua, Banksia marginata, Acacia mearnsii, A. longifolia, A. pycnantha, Clematis microphylla* and *Dodonea viscosa*, the under-storey had a diversity of unidentified small native ground species that were different between sites. Glenroy National Park is separated from the Coonawarra vineyards by a pine plantation (*Pinus radiata*) and grazing pasture, while Penola Conservation Park is separated by grazing pasture and mixed broad-acre cropping. The sentinel plants were placed in the Glenroy National Park and Penola Conservation Park, 25 m and 50 m respectively, in from the road that borders the southern perimeter of each park.

The Bond Rd site was a patch of established road side vegetation 15 m from vine yards (800 m west of the Messenger site) beside a dirt road (37º27' 18S 140º50' 34E) (**Treatment 2**). It was sheltered by a well-developed stand of *Acacia pycnantha* trees and the understorey was a mix of continuous pasture grasses, including *Phalaris* sp. The road was unsealed and the limestone surface was largely free of dust and particulate matter. This road was used infrequently compared to the Truck Stop site. The sentinel plants were placed 7 m from the eastern edge of the road and 1 m from the base of a stand of six *A. pycnantha* trees.

The Provis site was adjacent to a vineyard where a number of other experiments had been conducted as part of the broader study in previous seasons. The vineyard was bordered by 54 ha of largely undisturbed natural vegetation (37º12' 970S 140º52' 579E) (**Treatment 3**). This site was similar to Glenroy National Park and Penola Conservation Park sites, however the understorey was dominated by *Pteridium esculentum* (bracken fern). The sentinel plants were placed 2 m within the native vegetation and were 7 m away from the vines. This vineyard had a conservative fungicide and insecticide regime compared to the standard regional practice at the Messenger site (Table 6.5).

The Messenger site was a vineyard where a number of other experiments had been conducted as part of the broader study (37º21' 337S 140º50' 107E) (**Treatment 4**). This site represented a ‘standard’ vineyard environment with management practices that were common throughout vineyards within the Coonawarra (see Section 2.2.1). The sentinel plants were placed on a ‘headland’ surrounded by vines on three sides that were no more than 3 m away and vines to the south 30 m away. Although these plants would not receive direct fungicide sprays they may have been influenced by spray drift (Table 6.5).

Truck Stop site was centrally located in the Coonawarra vine growing area (37º29' 568S 140º83' 726E) (**Treatment 5**), and is situated on the western side of the Riddock Highway. Experimental plants were placed 10 m into a 0.25 ha area of four-year-old revegetation adjacent to the truck stop. The revegetation consisted of a mix of *Acacia* and *Eucalypt* species. The other three sides bordering the native vegetation comprised vineyards. The truck stop was unsealed with a high frequency of vehicular activity which created dust. This dust was evident on the sentinel plants after each experiment. The site was also exposed to weather due to the young age of the revegetation which had limited canopy development and were 1.5 m high. Site proximity to vines meant that the sentinel plants might also have been influenced by spray drift. The sentinel plants were placed 10 m from the edge of the truck park in the native revegetation.

Table 6-1 Sites used for the sentinel plant experiment and associated degree of disturbance from agricultural chemicals, physical disturbance, and degree of exposure. The higher the total points the more a site is disturbed. Refer to text for information on the ranking scale (section 6.2.1).

(Treatment no.) / Site	Site Characteristics	Chemical Fungicide / Insecticide	Physical disturbance raised dust	Degree of exposure to weather /wind	Total Points
1. Glenroy National Park	Undisturbed area of diverse native vegetation	-	-	1	1
1. Penola Conservation Park	Undisturbed area of diverse native vegetation	-	-	1	1
2. Bond Rd	Roadside *Acacia pycnantha* with undisturbed grass understorey	1	2	1	4
3. Provis	Native vegetation, bracken understorey	1	-	1	2
4. Messenger	Surrounded by vines, exposed to weather	2	1	3	6
5. Truck Stop	0.25 ha area of sparse native revegetation, adjacent vineyards, trees to 1.5m height	2	3	2	7

6.2.2 Host Plants for Sentinel Larvae

In the 2002-03 season, *E. postvittana* larvae were found on volunteer *Plantago* sp. in the region, indicating that this is a host plant. Seed was therefore collected from these plants and germinated in The University of Adelaide glasshouse. *Plantago* is easily grown so that sentinel potted plants could be standardised for age and quality.

Epiphyas postvittana eggs were obtained from the laboratory culture maintained by SARDI. Moths readily laid eggs on the inside of plastic drinking cups and egg masses were timed to emerge fortnightly for each repeat of the experiment. Prior to emergence, plastic spikes of 30 eggs were cut from the plastic cups and one spike was placed at the base of each plant. Neonate larvae were allowed to establish and feed for approximately 12 h before placing them in the field. Two potted (10 week old) *Plantago* plants, each with 30 neonate larvae were placed at the six sites. This was repeated seven times, every fortnight from 22 October 2004 until 23 January 2005.

At each site two pots were set up 2 m away from each other. The pots were placed in a 4 L plastic container that was filled with water, to prolong the health of the plant. The plastic container was staked at each corner with a 40 cm tent peg. Each potted sentinel plant was loosely surrounded with a wire mesh cylinder to reduce disturbance from vertebrate herbivores (e.g. rabbits and kangaroos). Potted sentinel plants were collected fortnightly and replaced with new pots and larvae. The collected pots from each site were taken back to the laboratory and larvae were placed in individual containers, given fresh foliage, numbered, reared through and parasitism recorded.

Pots at some sites were disturbed or damaged and so some data points are missing. At Glenroy National Park plants were destroyed on 3 December 2004 and 23 January 2005 by vertebrate herbivores. Plants at Penola Conservation Park were destroyed by people on the 23 January 2005. At the Messenger site on 17 December 2004, plants were exposed to herbicide and on the 29 of December 2004 at the Messenger and Truck Stop sites plants died from heat. Twenty-nine data points remained for the analysis.

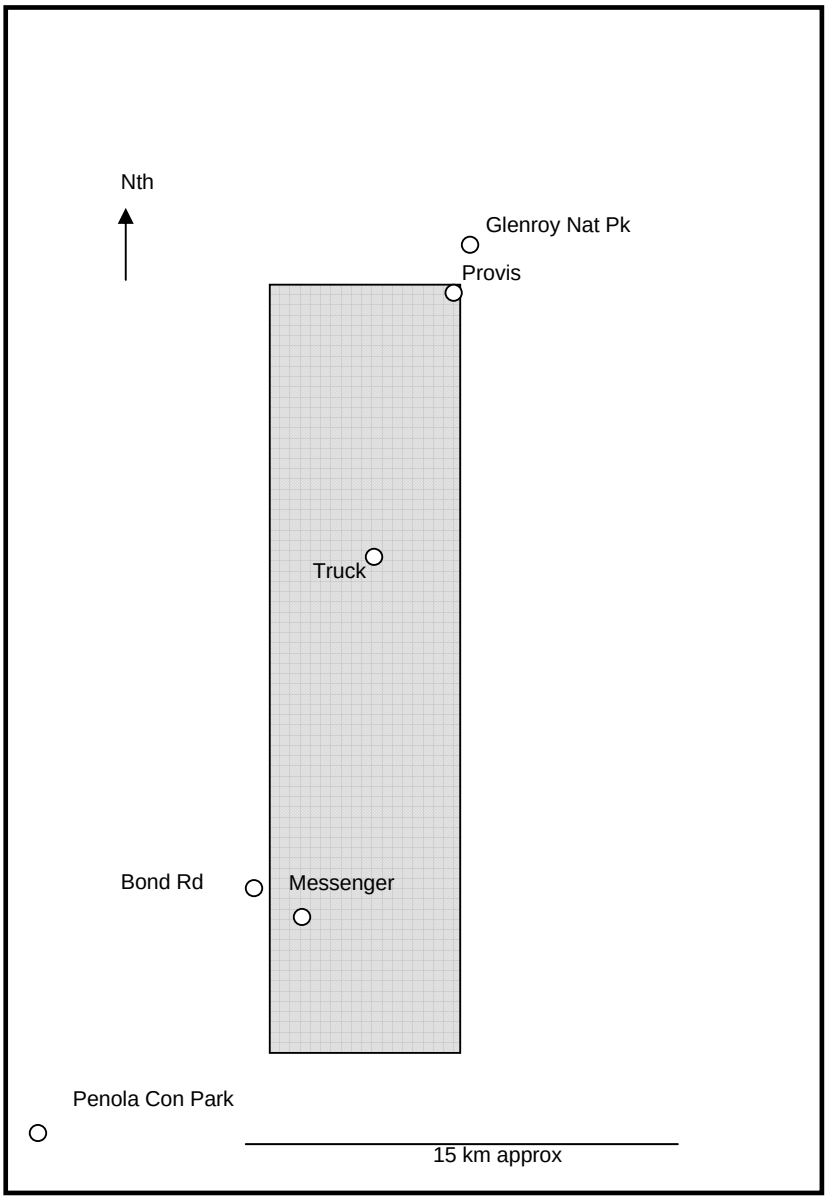


Figure 6-1 Schematic map showing location of sentinel plant sites. Shaded area denotes the extent of Coonawarra vineyards. Circles denote approx site and placement of sentinel plants.

6.3 DATA ANALYSIS

The data were pooled across dates due to the missing data and a *G* test for a 2x6 contingency table was used to determine any relationship between parasitism and site (Zar 1996). A post hoc, Tukey type procedure for testing multiple comparisons of proportions was used to determine which sites were significantly different from each other. This procedure uses the "q" statistic, the difference between sites divided by the standard error and the critical values for the q distribution at $\alpha = 0.05$ (Zar 1998).

6.4 RESULTS

Dolichogenidea tasmanica parasitised *E. postvittana* larvae at all sites except at the Truck Stop (Table 6.2). Parasitism by *D. tasmanica* was not independent of site (*G* 4176, *df* 5, *P* <0.05*)* as it was for parasitism by a second braconid wasp *Bassus* sp. (*G* 571.5, *df* 5, *P* <0.05*)*. Similar mean numbers of larvae were recollected from all of the sites except for Truck Stop (Table 6.2). Multiple comparisons of proportions confirmed this indicating parasitism by *D. tasmanica* was similar for all sites, except the Truck Stop which was significantly different (Table 6.3).

Bassus sp., was previously unrecorded from the Coonawarra region. It was recorded from three of the six sites; the Bond, Glenroy National Park and the Penola Conservation Park sites. Multiple comparisons of proportions confirmed that parasitism of *E. postvittana* by *Bassus* sp. was similar for three sites and that these sites were significantly different from the Messenger, Provis and Truck Stop, sites (Table 6.4**)**.

The highest parasitism for *D. tasmanica* and *Bassus* sp. combined, occurred at three sites, Penola Conservation Park 47.7%, Glenroy National Park 27.7% and Bond 25.2%(Table 6.2).

Table 6-2 The mean (**± SD)** number of sentinel *E. postvittana* larvae recollected, and parasitism by *Bassus* sp. and *D. tasmanica* for each site.

Treatment no. / Site	Mean (± SD) larvae recollected from each site	Total number recovered (%)	% Parasitism *Bassus* sp.	% Parasitism *D. tasmanica*
1. Glenroy National Pk	20.57 (± 17.62)	144 (16.60)	14.6	13.2
1. Penola Conserv. Pk	25.71 (± 24.47)	180 (20.74)	32.8	15.0
2. Bond	25.43 (± 14.77)	178 (20.50)	20.2	5.0
3. Provis	26.71 (± 5.50)	187 (21.54)	0.0	11.2
4. Messenger	8.14 (± 8.03)	57 (6.60)	0.0	19.3
5. Truck Stop	17.43 (± 13.90)	122 (14.06)	0.0	0.0

Table 6-3 Multiple comparisons for proportion of parasitism of *E.postvittana* larvae by *D. tasmanica*.

Site Comparison	Dif	SE	q	q 0.05,∞,6
Messenger				
vs Truck	23.8496	3.2383	7.3648	4.03
vs Provis	6.6718	3.0537	2.1848	4.03
Penola Conservation Pk				
vs Truck	20.3538	2.3713	8.5833	4.03
Glenroy National Park				
vs Truck	18.9252	2.4879	7.6069	4.03
Provis				
vs Truck	17.1778	2.3534	7.2991	4.03
Bond				
vs Truck	10.6903	2.3740	4.5031	4.03

Messenger	***a***
Penola Conservation Park	***a***
Glenroy National Park	***a***
Provis	***a***
Bond	***a***
Truck	***b***

Ranked transformed proportions were compared by comparing the largest proportion to the smallest in descending order. Comparisons where there were no differences are not represented.
Inset: Sites with different letters differed significantly based on multiple comparisons tests for proportions (P <0.05)

Table 6-4 Multiple comparisons for proportion of parasitism of *E. postvittana* larvae by *Bassus* sp.

Site Comparison	Dif	SE	q	q 0.05, ∞,6
Penola Conservation Pk				
vs Provis	32.8927	2.1152	15.5506	4.03
vs Truck	32.3973	2.3756	13.6375	4.03
vs Messenger	31.2113	3.0788	10.1375	4.03
vs Bond	8.2209	2.1383	3.8446	4.03
Bond				
vs Penola Con Pk	24.6717	2.1153	11.6634	4.03
vs Truck	24.1763	2.3740	10.1838	4.03
vs Messenger	22.9904	3.0696	7.4897	4.03
Messenger				
vs Provis	1.6813	3.0537	0.5505	4.03

Penola Conservation Park	***a***
Bond	***a***
Glenroy National Park	***a***
Messenger	***b***
Truck	***b***
Provis	***b***

Ranked transformed proportions were compared by comparing the largest proportion to the smallest in descending order. Comparisons where there were no differences are not represented.
Inset: Sites with different letters differed significantly based on multiple comparisons tests for proportions (P <0.05)

Table 6-5 Chemicals sprayed in vineyards at Provis and Messenger for 2004-05 season

Active Ingredient	Trade	Treatment 3 (Provis)	Treatment 4 (Messenger)
FUNGICIDES			
Elemental Sulphur	Thiovit	X	X
Trifloxystrobin	Flint	X	
Mancozeb + Metalaxyl	Ridomil		X
Mancozeb	Mancozeb		X
Copper oxychloride	Oxydul	X	X
Pyrimethanil	Scala	X	X
Penconazole	Topas		X
Triadimenol	Bayfidan		X
Iprodione	Rovral		X
INSECTICIDES			
Bt	Dipel	X	X
Indoxacarb	Avatar		X

6.5 DISCUSSION

Dolichogenidea tasmanica was widespread and occurred at all but one site. The second parasitoid, *Bassus* sp. had a more restricted distribution at this scale, occurring only at the least disturbed native vegetation sites.

The highest levels of parasitism were recorded at sites that were least disturbed and that comprised of native vegetation. While these results support the idea that the degree of disturbance may influence the occurrence of specific parasitoid species, there are a number of other factors that could also be influencing parasitism at the different sites. These factors include the types of and combination of disturbances, landscape fragmentation and vegetative diversity.

6.5.1 Disturbance

In vineyards throughout the year there are regular chemical and physical disturbances associated with wine grape production. Application of chemical insecticides and fungicides have been shown to influence and compromise the effectiveness of native parasitoids (van Driesche et al. 1998, Thomson et al. 2000). Several fungicides are used in Coonawarra vineyards for disease control (Table 6.5). Research by Thomson et al. (2000) has shown that the use of sulphur has a residual effect and is detrimental to all stages of the egg parasitoid *Trichogramma* sp. In field experiments where the fungicide Mancozeb® was removed, parasitism increased significantly especially for braconid species (van Driesche et al. 1998)

The use of chemical insecticides will reduce the numbers of parasitoids by virtue of killing them directly or their hosts, but it is not clear whether fungicides cause direct mortality to adult parasitoids or repel them. *Dolichogenidea tasmanica* occurred at all sites suggesting the use of chemicals in vineyards does not exclude them from these areas compared to *Bassus* sp. where chemicals may be responsible for its absence.

There are of course significant negative effects of insecticides on hosts and, as a consequence, parasitism. Non-target areas can also be affected by pesticide drift (Langhof et al. 2003). The Truck Stop and Messenger sites were adjacent to vineyards on three sides, so drift from chemical sprays may have contributed to the absence or low numbers of parasitoids.

There is some evidence that physical disturbance such as tilling can reduce parasitism (Thies and Tscharntke 1999) but the possible impacts of management activities in vineyards, such as brush mulching, pruning, harvesting and trimming on parasitoids and other natural enemies is unknown.

6.5.2 Cyclic Seasonal Disturbance

Disturbance may be interpreted in the context of seasonal change. Grapevines, despite their perennial framework, can be classed as ephemeral because they undergo seasonal change from spring growth to winter dormancy. During dormancy, vineyards are highly exposed to climatic extremes and provide no resources for parasitoids in the way of food, shelter and/or hosts. Thus, vineyards could be considered largely unsuitable for supporting populations of natural enemies such as parasitoids. This type of crop is ephemeral and therefore may require cyclical colonisation compared to perennial vegetation (Wissinger 1997). In comparison, there is little disturbance in native vegetation. Insects in native vegetation will be less exposed compared to those in vineyards especially at the beginning of the season, prior to grapevine canopy development. Native vegetation provides a diverse and highly complex non-deciduous vegetative habitat. These areas may afford insect species that live within them reduced

desiccation, shelter and buffering against extremes such as drought and flood. The idea that perennial non-crop habitat may provide important elements for the conservation of natural enemies is supported by the results presented in this study as well as a number of other studies (Dyer and Landis 1997, Peacor and Werner 2000, Hobbs and Cramer 2003).

It is likely that the absence of parasitoids at the Truck Stop site was due to a combination of factors including being highly exposed to the constant influence of raised dust (Bartlett 1951), drift from chemicals applied to adjacent vineyards, and being the furthest distance (compared to other locations) from either native remnant or source populations. Hot weather during the fifth replicate of the experiment (17 December 2004), resulted in plants at the more exposed Messenger and Truck Stop sites desiccating. They also had the lowest number of larvae. This suggests plants in less disturbed, less exposed areas may have been buffered from extreme temperatures and therefore remained healthy.

6.5.3 Fragmentation

Highly modified environments disrupt ecological interactions including ecosystem services (Thomas 1999, Denys and Tscharntke 2002, Tscharntke et al. 2002a, Cobbold et al. 2005). Disruption of food-web interactions can be explained by the decline in abundance and diversity of parasitoids when the area of suitable habitat is reduced (eg.Kruess and Tscharntke 2000) or fragmented (eg.Tscharntke et al. 2002b). Tscharntke and Kruess (1999b) suggest that crops such as grapevines leave de-faunated islands, that depend on non-crop habitat for recolonisation.. The Coonawarra vineyards have replaced extensive areas of largely non-deciduous perennial vegetation that are now only represented by the native vegetation present along roadsides, and at Penola Conservation Park and Glenroy National Park. Together with other surrounding habitats, the result is a highly fragmented landscape.

Results from field research support the notion that fragmentation reduces parasitism and that one key to limiting pest outbreaks is to increase areas of suitable habitat (Thies and Tscharntke 1999, Kruess and Tscharntke 2000, With et al. 2002, Cobbold et al. 2005). Previous studies have shown that natural enemies are influenced by the degree of fragmentation and proportion of suitable habitat within the landscape. Field experiments with two species of coccinellid, and their aphid prey in clover showed that the ratio of suitable habitat was more important than aggregation to prey in determining aphid suppression (With et al. 2002). For a given area, if suitable habitat (a patch) fell below 20% of the total area, it was isolated from natural enemies (With et al. 2002). Parasitism of the tortricid *Cydia nigricana*, in Europe was also shown to increase in larger areas of remnant habitat (Kruess and Tscharntke 2000). Further, the egg parasitoid *Ooencyrtus kuwanai* is known to resist moving across open spaces (Weseloh 1972). *Bassus* sp. may also resist moving from areas of

native vegetation if it perceives the area beyond as unsuitable. Alternatively, *D. tasmanica* may be more tolerant to such disturbances and fragmentation.

The current pattern of land use and landscape elements may mean that vineyards are too isolated from the resources that are required to support parasitoid species such as *Bassus* sp. and that the distance between them inhibit colonisation and recolonisation after a disturbance event from agronomic activities. Even though *Bassus* sp. occurred in native vegetation that was adjacent to vineyards, there was no evidence that it moved into vines indicating that there may be aspects of the vineyard environment that this species finds unfavourable.

6.5.4 Source and Sinks

Related to fragmentation is the idea that different areas may act as sources or sinks (Thomas 2001) (See also section 4.5.2). Sources are where parasitoid emigration exceeds immigration and births exceed deaths (Rosenheim 2001), and so maintain populations through colonisation (Pulliam 1988). Areas whereimmigration is greater than emigration are 'sinks.'

Vineyards may be acting as sinks in the beginning and middle of the season with parasitoid populations being unable to survive the period when vineyards are dormant, thus relying on annual colonisation. Research has also shown that the likelihood of recolonisation diminishes as a result of decreasing patch size of a source (Hanski 1998).

As for *D. tasmanica*, the results of this study support the idea that native vegetation may act as a source for *Bassus* sp. However, a combination of landscape fragmentation, disturbance, isolation and lack of recognition of vines as supporting hosts may discourage them from colonising the vineyards.

6.5.5 Vegetative Diversity

The 'enemies hypothesis' states that increased diversity of vegetation will result in a greater abundance of natural enemies, and therefore greater suppression of herbivore populations in polycultures compared to monocultures (Root 1973). This is thought to be because areas of increased vegetational diversity support a greater diversity of prey, more benign environmental conditions and a source of alternative food and/or hosts (Root 1973, Sheehan 1986, Andow 1991, Settle et al. 1996). However, results from previous research on this issue are varied (Andow 1991). For example, when comparing parasitism rates in complex versus simple agricultural landscapes, although it was expected that there would be more parasitism and parasitoids in the complex landscape, the results did not support this (Menalled et al. 2003). Alternatively, it has been demonstrated that parasitism of the spruce budworm was greater in areas with greater vegetational diversity (Cappuccino et al. 1998).

Results from this study indicate that *D. tasmanica* is ubiquitous across all sites but *Bassus* sp is found in more diverse and less disturbed native vegetation. Compared to the other native vegetation sites, the Provis site had a continuous understorey of bracken fern, that has been previously recorded as a host for *E. postvittana* (Shuter and Westoby 1992). The Provis site was 7 m away from a vineyard from which seven other primary parasitoids of *E. postvittana* were recorded in the same season. However it is interesting to note that the *Bassus* sp. was not recovered from the native vegetation at this site.

Successfully determining which habitat factors are influencing natural enemies is important to understand how these systems could be manipulated to improve pest management. An example of this is demonstrated by Murphy et al. (1998) who helped advance research initiated by Doutt and Nakata (1973) showing that diversifying vineyards by planting prune trees increased mortality of the pest grape leafhopper *Erythroneura elegantula* by the parasitoid *Anagrus epos*. The prune trees provided both overwintering habitat and hosts that allowed the parasitoid to survive and quickly colonise vines in spring. This research is an excellent example of where a specific type of vegetation planted near the target crop can have a profound effect on increasing pest suppression. The importance of specific habitat diversification is also similarly supported by other studies (Andow et al. 1997, Barbosa 1998, Baggen et al. 1999).

Before additional resources for parasitoids are provided consideration should be given to how these resources and the insects involved vary temporally (Menalled et al. 2003) and that not all resources are necessarily available or benefit specific parasitoids (Baggen et al. 1999). For example, when *Microctonus hyperodae*, a parasitoid of a stem weevil *Listronotus bonariensis*, was exposed to different flowers not all of them provided a benefit. In this case the parasitoid could not access the nectar of some plant species due to the morphology of floral inflorescences (Winkler et al. 2005, Vattala et al. 2006).

The concepts of scale and movement, i.e. how insects use resources in the landscape, also needs to be determined as this information is specific to a particular pest and its associated natural enemies. An example of species-specific parasitoid behaviour and the viability of host populations relative to areas of suitable habitat has been shown, where population dynamics depended on different geographic ranges of two different parasitoids (Hanski 1998, Van Nouhuys and Hanski 2002).

6.6 CONCLUSION

Dolichogenidea tasmanica may be a superior disperser compared with *Bassus* sp. and this study is the first to provide a preliminary understanding of the multiple habitats they use and how this may affect their time to colonise vineyards.

The results here suggest that the native parasitoid complex in this system is influenced by elements of the regional landscape including disturbance events and the presence or absence of native vegetation. Future research should focus on identifying and confirming whether or not vineyards rely on seasonal recolonisation. If this is the case, identifying the likely source populations, and understanding the influence of movement between the source (native vegetation or other crops) and sink (vineyards) on parasitoid and pest colonisation should be a research priority. While it is likely that native vegetation may be a source for *Bassus* sp., experiments will be required to establish where *D. tasmanica* first occurs. *Bassus* sp. has the potential to be an effective parasitoid but may be poorly adapted to agricultural conditions within the vineyard. The challenge for the future will therefore be to identify specific elements necessary for specific parasitoid species and to redesign, reintroduce and redevelop complexity and associated resilience into this agricultural system without reducing productivity.

There is no simple or set way to select the natural enemies that will have the greatest impact on a pest species. Instead it is an iterative process that involves designing different types of experiments at various scales and elucidating the biology of the species involved, testing the biological parameters of each species, and applying this knowledge to the system of interest (Levins and Wilson 1980, Luck et al. 1988, Langellotto and Denno 2004b). In order to advocate what vegetation design might encourage greater numbers of natural enemies such as *Bassus* sp. to move into crops, a deeper understanding of how these mobile insects respond to specific landscape resources and activities is needed.

CHAPTER 7

General Discussion

The production of Australian wine is a $4 billion industry and the fourth largest farm export crop nationally (AWBC 2004). *Epiphyas postvittana* is the most serious invertebrate pest in wine grape production especially in vineyards in southern Australia. The main aim of this thesis was to document the invertebrate species that inhabit Coonawarra vineyards and identify which of the natural enemies present may contribute to reducing *E. postvittana*. This was achieved successfully, in addition to a number of other aims which developed during the course of the research. This research also generated many new questions, which provide a set of clearly prioritised directions for future research.

An initial survey of Coonawarra vineyards provided an inventory of the arthropods and an opportunity to identify species of native natural enemies present in this system. These species were then assessed for their potential role in controlling *E. postvittana* (Chapter 2). Hymenopteran parasitoids are recognised for their close association with and their success in reducing various insect pests, i.e. they provide a valuable ecosystem service (Wilby and Thomas 2002). One of the most interesting results from the survey was identifying the diverse suite of Hymenoptera associated with *E. postvittana,* many of which were previously unknown. This work culminated in a taxonomic revision and collation of information about the parasitoid community associated with *E. postvittana* in Australia and included the description of a new hymenopteran species *Eriborus postvittana* (Ichneumonidae). This synopsis of *E. postvittana* parasitoids should provide an invaluable resource for future researchers and the viticulture industry.

Invertebrate pest populations are extremely variable, they are influenced by a range of different biotic and abiotic factors. In the case of *E. postvittana,* populations fluctuated between seasons, grapevine variety and sites. This study confirmed that there was a range of parasitoids present in vineyards, not all of these occurred at all of the sites and it is this difference that is particularly interesting. The site where most of the parasitoids species occurred was atypical compared to other vineyards in the region. This site had a more conservative pesticide management regime and was surrounded by a variety of land use. The site where most parasitoids occurred had consistently high levels of parasitism and a lower abundance of *E. postvittana* (Chapter 3). These results support the idea that natural enemies are influenced by biotic and abiotic factors within and beyond the crop. These factors may

include management activities, surrounding land use and/or proximity to source populations. An obvious extension of these results would be to isolate the mechanisms, which exclude parasitoids from many vineyards. Identifying these will provide opportunities for modifying viticutural management paractices to enhance the effectiveness of natural enemies in vineyards. Further study should also be undertaken to elucidate the biology and ecology of the many other parasitoid species in the system, other than *D. tasmanica,* the main species examined here.

Extensive field experiments showed that the response of *D. tasmanica* to the density of *E. postvittana* was inversely density-dependent. An inverse density-dependent response can result when the response of an individual or combined functional and/or numerical response of a population is not enough to compensate for the increase in pest population. Furthermore, the results suggest that this may be due to or the result of low numbers of *D. tasmanica*. Several factors might be involved here, for example, conditions that reduced their survival and/or reproduction. The isolation of vineyards from source populations may also result in insufficient numbers of *D. tasmanica* migrating into vineyards (Chapter 4). Determining the importance of these factors and their effect on parasitoid populations and quantifying parasitism as a result of increased parasitoid populations clearly warrants further research.

Interestingly, the experiments in Chapter 4 showed that grapevine variety was significantly influencing parasitism. *Epiphyas postvittana* larvae were always less abundant in Cabernet Sauvignon compared with Chardonnay vines, however the larvae collected from Cabernet Sauvignon were more likely to be parasitised compared with those in Chardonnay. Identifying such differences will be integral to developing sustainable management strategies. For example, planning the planting pattern of Cabernet Sauvignon across a region may act as a corridor and increase migration and penetration of parasitoids.

Agricultural and natural ecosystems comprise an infinite number of complex multi-species interactions (Rosenheim et al. 1995, Losey and Denno 1999, Rosenheim et al. 1999, Cardinale et al. 2003). The few that have been investigated indicate that more than one species of predator and/or parasitoid in an environment can have a range of effects on prey suppression. This research has identified a novel interaction between the predatory mite *A. baccarum,* the parasitoid *D. tasmanica* and *E. postvittana.* Results from laboratory experiments show that this interaction more often than not results in asymmetrical intraguild predation. Depending on the ratio of predatory mites to parasitoids, this interaction could have positive or negative implications for the suppression of *E. postvittana* (Chapter 5). These results will help to better understand and re-evaluate how the presence of multiple predatory species influence pest populations. This is significant in a broader ecological context,

contributing to the area of arthropod population dynamics. Attempts should now be made to see if similar results occur in vineyards.

There is body of research that shows that abiotic activities can disturb and decouple ecosystem services (Mooney et al. 1995a, Murphy et al. 1996, Duelli et al. 1999, Bommarco and Ekbom 2000, Carter 2001, Tscharntke et al. 2002a, Bianchi et al. 2006). A pilot experiment conducted at a landscape level quantified and compared parasitism between six sites. Each site was chosen and ranked according to the severity of disturbance it was likely to be subject to. Parasitism was highest for the areas that were least disturbed and no parasitism was recorded at the most disturbed site. A previously unrecorded braconid parasitoid, *Bassus* sp., parasitised *E. postvittana* in sites that were least disturbed, and these three sites also contained native vegetation. Isolating the type of disturbance and specific resources that are having the greatest influence on the presence and abundance of parasitoids should be a focus for future research. Host plants have been shown to significantly influence the behaviour of natural enemies. The effect the choice of host or sentinel plant has on the host and subsequent response of parasitoids should be given greater consideration when this type of experiment is conducted in future.

The conclusions for each chapter of this thesis point to biotic and abiotic factors directly affecting natural enemies via the ecological processes of birth, death, immigration and emigration. Chapters 4, 5 and 6 reach similar and somewhat related conclusions about the general factors most likely influencing the presence and abundance of parasitoids. These include two critical factors;

Disruption. The current configuration of vineyards representing a large area of deciduous monocrop, and surrounding land use, which may be effectively decoupling natural enemies from the host, *E. postvittana*. The use of chemicals for the control of vineyard pests and diseases are also likely to disrupt natural enemies.

Isolation. Parasitoid isolation from either resources, food, shelter and alternative hosts and/or from the source population all have the potential to affect migration, fecundity, longevity and abundance.

Successful biological control requires enhancing the effectiveness of natural enemies to reduce the density of pests. In order to achieve this, future research will be required to identify the specific factors and mechanisms that are likely to enhance the effectiveness of beneficial species. Isolating specific factors will facilitate the development of management practices to manipulate the environment with the aim of increasing the effectiveness of beneficial arthropods (Landis et al. 2000). There are a number of successful examples where important factors have been identified then addressed by restoring, reintroducing and integrating elements in various ways to enhance biological control by natural enemies (Bugg et al. 1987, Corbett and Plant 1993, Murphy et al. 1996, Bugg and Pickett 1998, Kogan et al. 1999, Landis et al. 2000, Martinsen et al. 2000, Hossain et al. 2001, Horton et al. 2002). However, there is little to be gained from manipulating a specific abiotic or biotic element if it is also advantageous to the pest or a factor, that has greater influence, is not addressed. Recently research has indicated that the provision of floral resources to enhance parasitism of *E. postvittana* by *D tasmanica* may not be as important as the presence of a regional source population (Bell et al. 2006).

The idea that there is a need to investigate and isolate specific mechanisms has been echoed by leading researchers who emphasise that the method and mechanism should be pursued instead of increasing diversity *per se*, to develop a progressive and robust science (Andow 1991, Corbett and Plant 1993, Schoenig et al. 1998, Schellhorn et al. 1999, Kennedy and Storer 2000, Landis et al. 2000, Zehnder et al. 2007). The results and implications of this study concur completely with this approach.

Results from this research have the potential to significantly contribute economically, socially, culturally and environmentally, in light of the impact the wine industry has on the Australian economy. Despite the research being conducted in the Coonawarra region, some of the results will undoubtedly be transferable to the wine industry nationally. For example, this research indicates that parasitoid *D. tasmanica* is present in a number of other vine growing regions in Australia. Management practices developed to increase the effectiveness of this parasitoid are likely to also be applicable in these areas. In early 2007 *E. postvittana* was first recorded in California, therefore research associated with *E. postvittana* and its associated natural enemies, including findings from this thesis, are likely to be increasingly relevant internationally.

These findings have significantly advanced our understanding of the biology and ecology of arthropods in viticultural ecosystems that had previously been lacking and/or poorly understood. This work has also shown that native hymenopteran parasitoids have far greater potential to reduce *E. postvittana* than has been realised to date. The results identify the areas where further research is required if their full potential, in providing a sustainable and effective ecosystem service, is to be exploited. These findings not only point to more sustainable ways of managing the major insect pest, light brown apple moth (*E. postvittana*), they also contribute to the scientific disciplines of ecology and entomology in a fundamental manner.

APPENDIX 1

Arthropod Survey

Identification and predatory biology of morphospecies recorded in the arthropod survey. Collected from five vineyard sites located in Coonawarra (see section 2.2.1 for details). Species for which only the order is given could not be identified further. Classification follows CSIRO (1991). NB: Biology, distinguishes predators from parasitoids using different symbols, p = predator and pa = parasitoid.

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
118	**ISOPODA**					
120	**CHILOPODA**					p
119	**DIPLOPODA**					
54	**ARANEAE**		Araneidae			p
385	**ARANEAE**		Araneidae			p
475	**ARANEAE**		Araneidae			p
454	**ARANEAE**		Araneidae			p
61	ARACHNIDA		Clubionidae			p
148	ARACHNIDA		Ctenidae			p
395	ARACHNIDA		Dictynidae			p
537	ARACHNIDA		Dipluridae			p
256	ARACHNIDA		Gnaphosidae			p
46	ARACHNIDA		Lycosidae			p
223	ARACHNIDA		Mimetidae			p
45	ARACHNIDA		Pholcidae			p
209	ARACHNIDA		Pisauridae			p
93	ARACHNIDA		Salticidae			p
483	ARACHNIDA		Salticidae			p
218	ARACHNIDA		Thomisidae			p
183	ARACHNIDA		Zodariidae			p
439	ARACHNIDA					p
520	**ACARI**	Mesostigmatid				
130	**ACARI**	Prostigmata	Anystidae	*Anystis*	*baccarum*	p
515	**ACARI**	Prostigmata	Anystidae	*Anystis*		p
127	**ACARI**	Prostigmata	Penthaleidae	*Halotydeus*	*destructor*	
117	**ACARI**	Prostigmata	Trombidiidae			p
128	**ACARI**	Prostigmata	Bdellidae			p
129	**ACARI**					
131	**ACARI**					
551	**ACARI**					
436	**ACARI**					
126	**COLLEMBOLA**					
541	**EPHEMEROPTERA**	Baetoidea	Baetidae			
23	**ORTHOPTERA**	Tetrigoidea				
562	ORTHOPTERA	Grylloidea	Gryllidae	*Teleogryllus*	*commodus*	
98	ORTHOPTERA	Grylloidea	Grillidae			
134	ORTHOPTERA	Grylloidea				
101	ORTHOPTERA					
282	ORTHOPTERA					
315	ORTHOPTERA					

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
525	ORTHOPTERA					
539	ORTHOPTERA					
138	DERMAPTERA	Forficuloidea	Anisolabididae			
352	DERMAPTERA	Forficuloidea	Anisolabididae			
33	DERMAPTERA	Forficuloidea	Forficulidae	*Forficula*	*auricularia*	
25	DERMAPTERA	Forficuloidea	Forficulidae			
115	DERMAPTERA	Forficuloidea	Labiduridae	*Labidura*	*truncata*	p
394	DERMAPTERA	Forficuloidea	Spongiphoridae			
168	DERMAPTERA					
484	**PSOCOPTERA**	Troctomorpha	Liposcelidae			
125	PSOCOPTERA					
202	PSOCOPTERA					
536	**HEMIPTERA**	Aleyrodoidea				
121	HEMIPTERA	Aphidoidea	Aphidae			
196	HEMIPTERA	Cercopoidea				
30	HEMIPTERA	Cicadelloidea	Cicadellidae			
94	HEMIPTERA	Cicadelloidea				
145	HEMIPTERA	Fulgoroidea	Delphacidae			
112	HEMIPTERA	Lygaeoidea	Lygaeidae	*Nysius*	*vinitor*	
20	HEMIPTERA	Lygaeoidea	Lygaeidae	*Pachybrachius*		
95	HEMIPTERA	Miroidea				
518	HEMIPTERA	Pentatomoidea	Cynidae			
62	HEMIPTERA	Psylloidea				
188	HEMIPTERA	Psylloidea				
548	HEMIPTERA	Psylloidea				
549	HEMIPTERA	Psylloidea				
550	HEMIPTERA	Psylloidea				
201	HEMIPTERA					
170	HEMIPTERA					
185	HEMIPTERA					
187	HEMIPTERA					
203	HEMIPTERA					
213	HEMIPTERA					
254	HEMIPTERA					
255	HEMIPTERA					
260	HEMIPTERA					
265	HEMIPTERA					
313	HEMIPTERA					
388	HEMIPTERA					
389	HEMIPTERA					
391	HEMIPTERA					
460	HEMIPTERA					
472	HEMIPTERA					
60	**THYSANOPTERA**					
122	THYSANOPTERA					
161	THYSANOPTERA					
34	**NEUROPTERA**	Hemerobioidea	Hemerobiidae			p
200	NEUROPTERA	Hemerobioidea	Hemerobiidae			p
565	NEUROPTERA	Hemerobioidea	Chrysopidae			p
564	NEUROPTERA	Mantispoidea	Mantispidae			p
184	COLEOPTERA	Caraboidea	Carabidae	*Clivina*	*quadratifrons*	p
252	COLEOPTERA	Caraboidea	Carabidae	*Notomus*		p
214	COLEOPTERA	Caraboidea	Carabidae	*Platisus*		p

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
49	COLEOPTERA	Caraboidea	Carabidae	*Pterostichinae*		p
181	COLEOPTERA	Caraboidea	Carabidae	*Promecoderus*	*concolor*	p
7	**COLEOPTERA**	Caraboidea	Carabidae	*Sarticus*	*discopunctatus*	p
24	COLEOPTERA	Caraboidea	Carabidae			p
457	COLEOPTERA	Caraboidea	Carabidae			p
77	COLEOPTERA	Chrysomeloidea				
288	COLEOPTERA	Cucujoidea	Coccinellidae	*Cocinella*	*transversalis*	p
279	COLEOPTERA	Cucujoidea	Coccinellidae	*Diomus*		p
68	COLEOPTERA	Cucujoidea	Coccinellidae	*Diomus*		p
362	COLEOPTERA	Cucujoidea	Coccinellidae	*Diomus*		p
212	COLEOPTERA	Cucujoidea	Coccinellidae	*Harmonia*	*conformis*	p
481	COLEOPTERA	Curculionoidea	Curculionidae	*Orthorhinus*	*klugi*	
42	COLEOPTERA	Curculionoidae	Curculionidae	*Otiorhynchus*	*cribricollis*	
226	COLEOPTERA	Cucujoidea	Cucujidae	*Platisus*		p
144	COLEOPTERA	Cucujoidea	Coccinellidae	*Scymnodes*		p
217	COLEOPTERA	Cucujoidea	Coccinellidae			p
330	COLEOPTERA	Cucujoidea	Coccinellidae			p
442	COLEOPTERA	Cucujoidea	Coccinellidae			p
163	COLEOPTERA	Cucujoidea	Coccinellidae			p
280	COLEOPTERA	Cucujoidea	Cocinellidae			p
482	COLEOPTERA	Curculionoidea	Curculionidae			
58	COLEOPTERA	Curculionoidea	Curculionidae			
63	COLEOPTERA	Curculionoidea	Curculionidae			
132	COLEOPTERA	Curculionoidea				
133	COLEOPTERA	Curculionoidea				
162	COLEOPTERA	Elateroidea	Elateridae			
505	COLEOPTERA	Elateroidea	Elateridae			
92	COLEOPTERA	Elateroidea				
12	COLEOPTERA	Staphylinoidea				
13	COLEOPTERA	Staphylinoidea				
27	COLEOPTERA	Staphylinoidea				
35	COLEOPTERA	Staphylinoidea				
76	COLEOPTERA	Staphylinoidea				
114	COLEOPTERA	Tenebrionoidea	Tenebrionidae			
56	COLEOPTERA					
66	COLEOPTERA					
80	COLEOPTERA					
91	COLEOPTERA					
100	COLEOPTERA					
108	COLEOPTERA					
109	COLEOPTERA					
110	COLEOPTERA					
111	COLEOPTERA					
116	COLEOPTERA					
136	COLEOPTERA					
137	COLEOPTERA					
140	COLEOPTERA					
141	COLEOPTERA					
149	COLEOPTERA					
150	COLEOPTERA					

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
176	COLEOPTERA					
177	COLEOPTERA					
180	COLEOPTERA					
182	COLEOPTERA					
189	COLEOPTERA					
190	COLEOPTERA					
205	COLEOPTERA					
210	COLEOPTERA					
216	COLEOPTERA					
222	COLEOPTERA					
225	COLEOPTERA					
227	COLEOPTERA					
228	COLEOPTERA					
229	COLEOPTERA					
244	COLEOPTERA					
245	COLEOPTERA					
261	COLEOPTERA					
264	COLEOPTERA					
281	COLEOPTERA					
283	COLEOPTERA					
312	COLEOPTERA					
351	COLEOPTERA					
359	COLEOPTERA					
379	COLEOPTERA					
390	COLEOPTERA					
435	COLEOPTERA					
461	COLEOPTERA					
462	COLEOPTERA					
471	COLEOPTERA					
490	COLEOPTERA					
491	COLEOPTERA					
495	COLEOPTERA					
511	COLEOPTERA					
540	COLEOPTERA					
566	**DIPTERA**	Asiloidea	Asilidae			p
8	DIPTERA	Brachycera	Calliphoridae			
123	DIPTERA	Brachycera				
153	DIPTERA	Empidoidea	Empididae			p
124	DIPTERA	Nematocera				
18	DIPTERA	Nemetocera	Trichoceridae			p
192	DIPTERA	Oestroidea	Tachinidae	*Voriella*	*uniseta*	pa
152	DIPTERA	Stratiomyoidea	Stratiomyidae	*Odontomyia*	*amyris*	
14	DIPTERA	Syrphoidea	Syrphidae	*Melangyna*	*viridiceps*	p
158	DIPTERA					
159	DIPTERA					
316	DIPTERA					
469	DIPTERA					
523	DIPTERA					
546	DIPTERA					
169	**LEPIDOPTERA**	Noctuoidea	Agaristidae	*Phalenoides*	*glycine*	
243	LEPIDOPTERA	Papilionoidea	Pieridae	*Pieris*	*rapae*	

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
194	LEPIDOPTERA	Tortricoidea	Tortricidae			
193	LEPIDOPTERA	Tortricoidea	Tortricidae	*Epiphyas*	*postvittana*	
464	LEPIDOPTERA	Tortricoidea	Tortricidae	*Merophyas*	*divulsana*	
267	LEPIDOPTERA	Yponomeutoidea	Glyphipterigidae	*Tebenna*	*bradleyi micalis*	
175	LEPIDOPTERA	Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*	
468	LEPIDOPTERA					
516	LEPIDOPTERA					
86	HYMENOPTERA	Apoidea	Apidae	*Apis*	*mellifera*	
552	**HYMENOPTERA**	Apoidea	Colletidae	*Hylaeus*		
556	HYMENOPTERA	Apoidea	Colletidae			
26	HYMENOPTERA	Apoidea	Halicidae			
41	HYMENOPTERA	Apoidea				
43	HYMENOPTERA	Apoidea				
47	HYMENOPTERA	Apoidea				
59	HYMENOPTERA	Apoidea				
102	HYMENOPTERA	Apoidea				
139	HYMENOPTERA	Apoidea				
191	HYMENOPTERA	Apoidea				
253	HYMENOPTERA	Apoidea				
311	HYMENOPTERA	Apoidea				
458	HYMENOPTERA	Apoidea				
547	HYMENOPTERA	Apoidea				
206	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
32	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
78	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
81	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
99	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
107	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
230	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
240	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
287	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
300	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
301	HYMENOPTERA	Ceraphronoidea	Ceraphronidae			pa
84	HYMENOPTERA	Ceraphronoidea	Megaspilidae			pa
135	HYMENOPTERA	Ceraphronoidea	Megaspilidae			pa
57	HYMENOPTERA	Ceraphronoidea	Megaspilidae			pa
257	HYMENOPTERA	Ceraphronoidea	Megaspilidae			pa
303	HYMENOPTERA	Ceraphronoidea				pa
306	HYMENOPTERA	Ceraphronoidea				pa
320	HYMENOPTERA	Ceraphronoidea				pa
321	HYMENOPTERA	Ceraphronoidea				pa
322	HYMENOPTERA	Ceraphronoidea				pa
323	HYMENOPTERA	Ceraphronoidea				pa
331	HYMENOPTERA	Ceraphronoidea				pa
332	HYMENOPTERA	Ceraphronoidea				pa
366	HYMENOPTERA	Ceraphronoidea				pa
380	HYMENOPTERA	Ceraphronoidea				pa
381	HYMENOPTERA	Ceraphronoidea				pa
392	HYMENOPTERA	Ceraphronoidea				pa
406	HYMENOPTERA	Ceraphronoidea				pa
407	HYMENOPTERA	Ceraphronoidea				pa

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
408	HYMENOPTERA	Ceraphronoidea				pa
409	HYMENOPTERA	Ceraphronoidea				pa
420	HYMENOPTERA	Ceraphronoidea				pa
431	HYMENOPTERA	Ceraphronoidea				pa
501	HYMENOPTERA	Ceraphronoidea				pa
513	HYMENOPTERA	Ceraphronoidea				pa
526	HYMENOPTERA	Ceraphronoidea				pa
557	HYMENOPTERA	Ceraphronoidea				pa
219	HYMENOPTERA	Chalcidoidea	Aphelinidae			pa
231	HYMENOPTERA	Chalcidoidea	Aphelinidae			pa
246	HYMENOPTERA	Chalcidoidea	Aphelinidae			pa
275	HYMENOPTERA	Chalcidoidea	Aphelinidae			pa
31	HYMENOPTERA	Chalcidoidea	Aphelinidae			pa
71	HYMENOPTERA	Chalicidoidea	Aphelinidae			pa
579	HYMENOPTERA	Chalcidoidea	Chalcididae	*Brachymeria*		pa
574	HYMENOPTERA	Chalcidoidea	Chalcididae	*Brachymeria*	*phya*	pa
353	HYMENOPTERA	Chalcidoidea	Chalcididae			
354	HYMENOPTERA	Chalcidoidea	Chalcididae			
363	HYMENOPTERA	Chalcidoidea	Chalcididae			
575	HYMENOPTERA	Chalcidoidea	Elasmidae	*Elasmus*		pa
6	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
88	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
156	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
166	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
178	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
235	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
294	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
307	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
347	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
356	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
372	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
417	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
450	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
563	HYMENOPTERA	Chalcidoidea	Encyrtidae			pa
383	HYMENOPTERA	Chalcidoidea	Eucharitidae			pa
4	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
50	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
179	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
232	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
238	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
239	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
276	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
277	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
278	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
393	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
413	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
416	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
452	HYMENOPTERA	Chalcidoidea	Eulophidae			pa
52	HYMENOPTERA	Chalicidoidea	Eulophidae			pa
329	HYMENOPTERA	Chalcidoidea	Eupelmidae			pa
157	HYMENOPTERA	Chalcidoidea	Eurytomidae			pa

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
198	HYMENOPTERA	Chalcidoidea	Eurytomidae			pa
248	HYMENOPTERA	Chalcidoidea	Eurytomidae			pa
365	HYMENOPTERA	Chalcidoidea	Eurytomidae			pa
96	HYMENOPTERA	Chalcidoidea	Mymaridae			pa
220	HYMENOPTERA	Chalcidoidea	Mymaridae			pa
268	HYMENOPTERA	Chalcidoidea	Mymaridae			pa
293	HYMENOPTERA	Chalcidoidea	Mymaridae			pa
382	HYMENOPTERA	Chalcidoidea	Mymaridae			pa
444	HYMENOPTERA	Chalcidoidea	Mymaridae			pa
154	HYMENOPTERA	Chalcidoidea	Mymarommatidae			pa
580	HYMENOPTERA	Chalcidoidea	Perilampidae	*Perilampus*		pa
174	HYMENOPTERA	Chalcidoidea	Perilampidae			pa
371	HYMENOPTERA	Chalcidoidea	Perilampidae			pa
97	HYMENOPTERA	Chalcidoidea	Pteromalidae			pa
398	HYMENOPTERA	Chalcidoidea	Pteromalidae			pa
470	HYMENOPTERA	Chalcidoidea	Pteromalidae			pa
451	HYMENOPTERA	Chalcidoidea	Signiphoridae			pa
328	HYMENOPTERA	Chalcidoidea	Tanaostigmatidae			pa
234	HYMENOPTERA	Chalcidoidea	Tetracampidae			pa
384	HYMENOPTERA	Chalcidoidea	Tetracampidae			pa
207	HYMENOPTERA	Chalcidoidea	Torymidae			pa
561	HYMENOPTERA	Chalcidoidea	Torymidae			pa
424	HYMENOPTERA	Chalcidoidea	Torymidae			pa
576	HYMENOPTERA	Chalcidoidea	Trichogrammatidae	*Trichogramma*		pa
53	HYMENOPTERA	Chalcidoidea	Trichogrammatidae			pa
318	HYMENOPTERA	Chalcidoidea	Trichogrammatidae			pa
339	HYMENOPTERA	Chalcidoidea	Trichogrammatidae			pa
340	HYMENOPTERA	Chalcidoidea	Trichogrammatidae			pa
375	HYMENOPTERA	Chalcidoidea				pa
533	HYMENOPTERA	Chalcidoidea				pa
90	HYMENOPTERA	Chalcidoidea				pa
172	HYMENOPTERA	Chalcidoidea				pa
237	HYMENOPTERA	Chalcidoidea				pa
335	HYMENOPTERA	Chalcidoidea				pa
399	HYMENOPTERA	Chalcidoidea				pa
402	HYMENOPTERA	Chalcidoidea				pa
418	HYMENOPTERA	Chalcidoidea				pa
419	HYMENOPTERA	Chalcidoidea				pa
425	HYMENOPTERA	Chalcidoidea				pa
465	HYMENOPTERA	Chalcidoidea				pa
488	HYMENOPTERA	Chalcidoidea				pa
489	HYMENOPTERA	Chalcidoidea				pa
497	HYMENOPTERA	Chalcidoidea				pa
498	HYMENOPTERA	Chalcidoidea				pa
500	HYMENOPTERA	Chalcidoidea				pa
509	HYMENOPTERA	Chalcidoidea				pa
510	HYMENOPTERA	Chalcidoidea				pa
522	HYMENOPTERA	Chalcidoidea				pa
528	HYMENOPTERA	Chalcidoidea				pa
530	HYMENOPTERA	Chalcidoidea				pa
531	HYMENOPTERA	Chalcidoidea				pa

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
532	HYMENOPTERA	Chalcidoidea				pa
535	HYMENOPTERA	Chalcidoidea				pa
543	HYMENOPTERA	Chalcidoidea				pa
553	HYMENOPTERA	Chalcidoidea				pa
558	HYMENOPTERA	Chalcidoidea				pa
1	HYMENOPTERA	Chrysidoidea	Bethylidae	*Eupsenella*		pa
242	HYMENOPTERA	Chrysidoidea	Bethylidae	*Goniozus*		pa
364	HYMENOPTERA	Chrysidoidea	Bethylidae	*Goniozus*		pa
577	HYMENOPTERA	Chrysidoidea	Bethylidae	*Goniozus*		pa
578	HYMENOPTERA	Chrysidoidea	Bethylidae	*Goniozus*		pa
410	HYMENOPTERA	Chrysidoidea	Bethylidae	*Sierola*		pa
559	HYMENOPTERA	Chrysidoidea	Bethylidae	*Sierola*		pa
29	HYMENOPTERA	Chrisidoidea	Bethylidae			pa
208	HYMENOPTERA	Chrysidoidea	Bethylidae			pa
338	HYMENOPTERA	Chrysidoidea	Bethylidae			pa
317	HYMENOPTERA	Chrysidoidea	Bethylidae			pa
355	HYMENOPTERA	Chrysidoidea	Bethylidae			pa
113	HYMENOPTERA	Chrysidoidea	Chrysididae			pa
476	HYMENOPTERA	Chrysidoidea	Drynidae			pa
360	HYMENOPTERA	Chrysidoidea				pa
186	HYMENOPTERA	Cynipoidea	Charipidae			pa
75	HYMENOPTERA	Cynipoidea	Cnipidae			pa
82	HYMENOPTERA	Cynipoidea	Figitidae			pa
89	HYMENOPTERA	Cynipoidea	Ibaliidae			pa
343	HYMENOPTERA	Cynipoidea				pa
344	HYMENOPTERA	Cynipoidea				pa
374	HYMENOPTERA	Cynipoidea				pa
512	HYMENOPTERA	Cynipoidea				pa
573	HYMENOPTERA	Ichneumonoidea	Braconidae	*Bassus*		pa
3	HYMENOPTERA	Ichnuemonoidea	Braconidae	*Dolichogenidea*	*tasmanica*	pa
19	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
103	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
104	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
105	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
155	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
195	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
221	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
247	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
291	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
292	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
302	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
415	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
429	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
466	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
514	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
517	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
521	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
527	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
534	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa
542	HYMENOPTERA	Ichnuemonoidea	Braconidae			pa

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
197	HYMENOPTERA	Ichnuemonoidea	Broconidae			
569	HYMENOPTERA	Ichneumonoidea	Ichneumonidae	*Australoglypta*	*latrobei*	pa
266	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae	*Diadegma*		
567	HYMENOPTERA	Ichneumonoidea	Ichneumonidae	*Eriborus*	*epiphyas*	pa
570	HYMENOPTERA	Ichneumonoidea	Ichneumonidae	*Euceros*		pa
581	HYMENOPTERA	Ichneumonoidea	Ichneumonidae	*Labium*		pa
571	HYMENOPTERA	Ichneumonoidea	Ichneumonidae	*Netelia*		pa
572	HYMENOPTERA	Ichneumonoidea	Ichneumonidae	*Plectochorus*		pa
568	HYMENOPTERA	Ichneumonoidea	Ichneumonidae	*Temalucha*	*minuta*	pa
44	HYMENOPTERA	Ichnuemonoidea	Ichneumonidae			pa
69	HYMENOPTERA	Ichnuemonoidea	Ichneumonidae			pa
85	HYMENOPTERA	Ichnuemonoidea	Ichneumonidae			pa
106	HYMENOPTERA	Ichnuemonoidea	Ichneumonidae			pa
171	HYMENOPTERA	Ichneumonoidea	Ichnuemonidae			pa
5	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
151	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
224	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
241	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
284	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
289	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
290	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
370	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
377	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
405	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
414	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
467	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
485	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
199	HYMENOPTERA	Ichnuemonoidea	Ichnuemonidae			pa
421	HYMENOPTERA	Platygasteroidea	Platygastridae			pa
250	HYMENOPTERA	Platygasteroidea	Platygastridae			pa
285	HYMENOPTERA	Platygasteroidea	Scelionidae	*Baeini*		pa
304	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
305	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
309	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
310	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
327	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
333	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
361	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
367	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
368	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
373	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
403	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
36	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
2	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
64	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
87	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
142	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
143	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
165	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
173	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
233	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
236	HYMENOPTERA	Platygasteroidea	Scelionidae			pa

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
262	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
270	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
271	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
272	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
274	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
286	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
260	HYMENOPTERA	Platygasteroidea	Scelionidae			pa
167	HYMENOPTERA	Platygasteroidea				pa
319	HYMENOPTERA	Platygasteroidea				pa
326	HYMENOPTERA	Platygasteroidea				pa
334	HYMENOPTERA	Platygasteroidea				pa
341	HYMENOPTERA	Platygasteroidea				pa
342	HYMENOPTERA	Platygasteroidea				pa
345	HYMENOPTERA	Platygasteroidea				pa
358	HYMENOPTERA	Platygasteroidea				pa
411	HYMENOPTERA	Platygasteroidea				pa
412	HYMENOPTERA	Platygasteroidea				pa
427	HYMENOPTERA	Platygasteroidea				pa
428	HYMENOPTERA	Platygasteroidea				pa
445	HYMENOPTERA	Platygasteroidea				pa
446	HYMENOPTERA	Platygasteroidea				pa
447	HYMENOPTERA	Platygasteroidea				pa
448	HYMENOPTERA	Platygasteroidea				pa
449	HYMENOPTERA	Platygasteroidea				pa
455	HYMENOPTERA	Platygasteroidea				pa
456	HYMENOPTERA	Platygasteroidea				pa
459	HYMENOPTERA	Platygasteroidea				pa
478	HYMENOPTERA	Platygasteroidea				pa
479	HYMENOPTERA	Platygasteroidea				pa
480	HYMENOPTERA	Platygasteroidea				pa
486	HYMENOPTERA	Platygasteroidea				pa
487	HYMENOPTERA	Platygasteroidea				pa
492	HYMENOPTERA	Platygasteroidea				pa
529	HYMENOPTERA	Platygasteroidea				pa
554	HYMENOPTERA	Platygasteroidea				pa
555	HYMENOPTERA	Platygasteroidea				pa
269	HYMENOPTERA	Platygasteroidea				pa
211	HYMENOPTERA	Platygasteroidea				pa
502	HYMENOPTERA	Platygasteroidea				pa
503	HYMENOPTERA	Platygasteroidea				pa
504	HYMENOPTERA	Platygasteroidea				pa
51	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
70	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
73	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
74	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
273	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
295	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
296	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
297	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
298	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
299	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
83	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
369	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
308	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
336	HYMENOPTERA	Proctotrupoidea	Diapriidae			pa
28	HYMENOPTERA	Proctotrupoidea				pa
249	HYMENOPTERA	Proctotrupoidea				pa

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
426	HYMENOPTERA	Proctotrupoidea				pa
453	HYMENOPTERA	Proctotrupoidea				pa
544	HYMENOPTERA	Proctotrupoidea				pa
545	HYMENOPTERA	Proctotrupoidea				pa
560	HYMENOPTERA	Proctotrupoidea				pa
376	HYMENOPTERA	Proctotrupoidea				pa
258	HYMENOPTERA	Proctotrupoidea				pa
346	HYMENOPTERA	Proctotrupoidea				pa
357	HYMENOPTERA	Proctotrupoidea				pa
477	HYMENOPTERA	Proctotrupoidea				pa
538	HYMENOPTERA	Proctotrupoidea				p
519	HYMENOPTERA	Sphecoidea	Sphecidae			p
146	HYMENOPTERA	Sphecoidea	Sphecidae			p
396	HYMENOPTERA	Sphecoidea	Sphecidae			P
443	HYMENOPTERA	Sphecoidea	Sphecidae			p
263	HYMENOPTERA	Sphecoidea	Sphecidae			p
17	HYMENOPTERA	Vespoidea	Formicidae	*Iridomymex*		p
21	HYMENOPTERA	Vespoidea	Formicidae	*Monomorium*		p
16	HYMENOPTERA	Vespoidea	Formicidae	*Myrmecia*		p
22	HYMENOPTERA	Vespoidea	Formicidae	*Notoncus*		p
11	HYMENOPTERA	Vespoidea	Formicidae	*Paratrechina*		p
37	HYMENOPTERA	Vespoidea	Formicidae	*Pheidole*		p
38	HYMENOPTERA	Vespoidea	Formicidae	*Pheidole*		p
39	HYMENOPTERA	Vespoidea	Formicidae	*Pheidole*		p
40	HYMENOPTERA	Vespoidea	Formicidae	*Pheidole*		p
9	HYMENOPTERA	Vespoidea	Formicidae	*Rhytidoponera*		p
10	HYMENOPTERA	Vespoidea	Formicidae			p
15	HYMENOPTERA	Vespoidea	Formicidae			p
147	HYMENOPTERA	Vespoidea	Formicidae			p
337	HYMENOPTERA	Vespoidea	Formicidae			p
348	HYMENOPTERA	Vespoidea	Formicidae			p
349	HYMENOPTERA	Vespoidea	Formicidae			p
350	HYMENOPTERA	Vespoidea	Formicidae			p
378	HYMENOPTERA	Vespoidea	Formicidae			p
386	HYMENOPTERA	Vespoidea	Formicidae			p
397	HYMENOPTERA	Vespoidea	Formicidae			p
400	HYMENOPTERA	Vespoidea	Formicidae			p
401	HYMENOPTERA	Vespoidea	Formicidae			p
432	HYMENOPTERA	Vespoidea	Formicidae			p
433	HYMENOPTERA	Vespoidea	Formicidae			p
440	HYMENOPTERA	Vespoidea	Formicidae			p
441	HYMENOPTERA	Vespoidea	Formicidae			p
17b	HYMENOPTERA	Vespoidea	Formicidae			p
48	HYMENOPTERA	Vespoidea	Formicidae			p
55	HYMENOPTERA	Vespoidea	Formicidae			p
65	HYMENOPTERA	Vespoidea	Formicidae			p
79	HYMENOPTERA	Vespoidea	Formicidae			p
215	HYMENOPTERA	Vespoidea	Formicidae			p
251	HYMENOPTERA	Vespoidea	Formicidae			p
259	HYMENOPTERA	Vespoidea	Formicidae			p
430	HYMENOPTERA	Vespoidea	Formicidae			p
506	HYMENOPTERA	Vespoidea	Formicidae			p

Morpho species no	Order	Superfamily	Family	Genus	Species	Biology
507	HYMENOPTERA	Vespoidea	Formicidae			p
508	HYMENOPTERA	Vespoidea	Formicidae			p
473	HYMENOPTERA	Vespoidea	Mutillidae			p
524	HYMENOPTERA	Vespoidea	Mutillidae			p
422	HYMENOPTERA	Vespoidea	Pompilidae			p
474	HYMENOPTERA	Vespoidea	Tiphiidae			p
67	HYMENOPTERA	Vespoidea				p
404	HYMENOPTERA	Vespoidea				p
423	HYMENOPTERA	Vespoidea				p
434	HYMENOPTERA	Vespoidea				p
463	HYMENOPTERA	Vespoidea				p
496	HYMENOPTERA	Vespoidea				p
499	HYMENOPTERA					
324	HYMENOPTERA					
72	HYMENOPTERA					
160	HYMENOPTERA					
164	HYMENOPTERA					
204	HYMENOPTERA					
314	HYMENOPTERA					
325	HYMENOPTERA					
437	HYMENOPTERA					
438	HYMENOPTERA					
493	HYMENOPTERA					
494	HYMENOPTERA					

The Hymenopteran Parasitoids of Light Brown Apple Moth, *Epiphyas postvittana* (Walker)(Lepidoptera: Tortricidae) in Australia.

The hymenopteran parasitoids of light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) in Australia.

Cate Paull and Andrew D Austin

Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Sciences, Darling Building, The University of Adelaide, Adelaide, SA 5005, Australia.

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Paull, C. (Candidate)
Organised and conducted fieldwork, examined parasitoid specimens, interpreted data and wrote the manuscript.

Austin, A.D.
Sought and won funding, supervised development of work, checked parasitoid identification, described the new species and edited draft manuscript.

I give consent for C. Paull to present this paper for examination towards the degree of Doctor of Philosophy.

Signed: Date: 14 December 2007

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