The Non-Target Effects of the Introduced Parasitoid *Trigonospila brevifacies* (Hardy) (Diptera:Tachinidae) on the Native Fauna of New Zealand.

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Vanessa M.W. Munro

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This work is dedicated to Jock McLauchlan.

Difficulties encountered on a journey provide the traveller with enlightenment.
(Tibetan proverb).

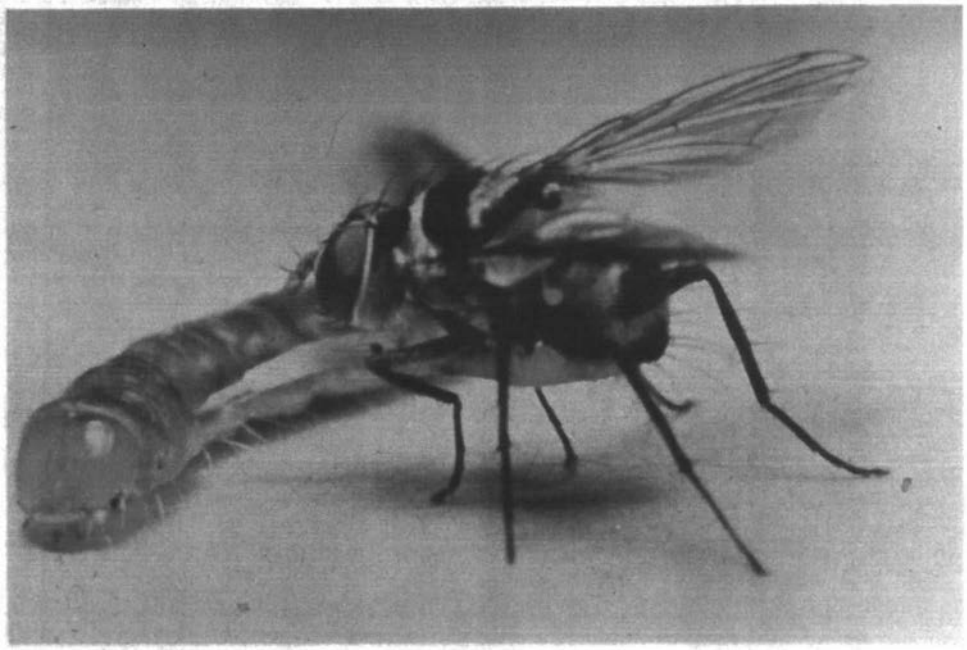

Plate 1. Female *Trigonospila brevifacies* ovipositing on a late-instar tortricid larva in the laboratory (courtesy of Hort Research Ltd.).

Plate 2. Male *Trigonospila brevifacies* in the field, one of three males observed in a lek.

ABSTRACT

The Australian tachinid parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) was introduced to New Zealand 30 years ago as a biological control for the exotic orchard pest *Epiphyas postvittana* Walker (Lepidoptera: Tortricidae). *Trigonospila brevifacies*, an endoparasitoid of late-instar lepidopteran larvae, was introduced concurrently with *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae), a parasitoid of lepidopteran pupae. *Trigonospila brevifacies* is now known to attack several non-target pest and non-pest lepidopteran species.

The impact of *T. brevifacies* on non-target fauna was investigated. Life history data (i.e., longevity, fecundity, productivity and sex ratio) for *T. brevifacies* were quantified in the laboratory. These data and field data were used to investigate whether superparasitism is an adaptive reproductive strategy for this species by comparing the return in adult progeny per egg for single and multiple egg clutches. Superparasitism may be advantageous for the survival of rare non-target hosts.

Data from a two-year, six-site survey of native forests determined that *T. brevifacies* attacked eight non-target Lepidoptera. The characteristic common to the phylogenetically diverse host group was that all are concealed feeders. Laboratory testing showed that pre-imaginal conditioning of parasitoid larvae did not confer adults with a preference for the host species in which they were reared.

Quantitative food web data from a two-year field survey showed that *T. brevifacies* was the numerically dominant parasitoid of the species attacking native Tortricidae at sub-canopy levels and that it competed for hosts with 12 native and one other introduced species of parasitoid.

The abundance of larval hosts and *T. brevifacies* was compared between the edges and centres of forest patches. Host density was determined by quadrat counts and parasitoid abundance by sticky traps. Both larval hosts and the parasitoid were more abundant at the forest edge. Trap hosts were also used to quantify parasitism levels along edge to forest-centre tansects. Parasitism by *T. brevifacies* was highest at forest edges declining to almost zero at 30m into a forest, indicating that forest centres with continuous canopy should offer hosts' refuge from *T. brevifacies* parasitism.

Archival and field data were used to determine the present geographical ranges of *T. brevifacies* and *X. rhopaloceros* and climatic data were used to predict where else in New Zealand these two parasitoids are likely to colonise in the future.

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Defining biological control

Classical biological control is defined as the deliberate release of a predator, parasite or pathogen into a new geographical location to control a weed or pest which is exotic, and sometimes native, to that location (DeBach, 1974; DeBach & Rosen, 1991; Van Driesche & Bellows, 1996) with the purpose of reducing the pest population to levels below an economic damage threshold (Samways, 1988). The biocontrol agent may be released in crop systems or in native habitats depending on where the target species is causing damage (Van Driesche, 1994). Classical biocontrol is mostly thought of as the introduction of arthropod predators and parasitoids, but can also include other categories of beneficial species such as; dung beetles to reduce breeding sites of dipteran pests of livestock (Cameron *et al.*, 1987); and species to compete for resources with pest species (Moon, 1980). The term neoclassical biological control is used when exotic biocontrol agents are introduced to target a pest species which is native to that location (Simberloff, 1992). The premise of neoclassical biological control is based on the new associations hypothesis, where the lack of co-evolutionary history between pest and enemy species supposedly makes the enemy species a more effective biocontrol agent (Hokkanen & Pimentel, 1989).

The use of natural enemies to control pest species was practiced by ancient cultures, but recent classical biological control began in the latter part of the 19th century (Caltagirone, 1981). New Zealand was the source of the vedalia lady beetle (*Rodolia cardinalis* (Mulsant)), an Australian coccinellid, used in the first classical biocontrol programme when this predator was introduced to California to control the cottony-cushion scale (*Icerya purchasi* Maskell) on citrus in 1889 (Caltagirone, 1981). Biocontrol agents are often used to combat invasions by exotic species that pose a threat to agriculture, horticulture, the environment or public health. Invasions include, the deliberate release of species in new locations that become pests, accidental introduction where human activity inadvertently disperses organisms to new geographical locations (Van Driesche & Hoddle, 1997), and dispersal of new species by their own volition, such as the trans-Tasman dispersal of Australian insects to New Zealand (Fox, 1974).

Successful international biocontrol programmes

Instances of successful biocontrol programmes have been documented where pests have been eradicated or reduced to below economic damage thresholds in commercially valuable agricultural, horticultural and forestry sectors. The Australian coccinellid *R. cardinalis,* a predator of the Australian cottony cushion scale (*I. purchasi*), controls this pest in the USA (Bartlett, 1978). The Argentinean pyralid moth, *Cactoblastis cactorum*, controlled the prickly pear (*Opuntia* spp), a plant pest in agricultural grasslands of Australia (Clausen, 1978). A tachinid, *Bessia remota* Aldrich, introduced from Malaysia, to Fiji, caused the extinction of its target species, the coconut moth, *Levuana iridescens* Bethune-Baker, an endemic pest (Rao *et al.*, 1971). However, of the entomophagous biocontrol agents released worldwide between 1880 and 1989, only 5-15 % successfully controlled their target pest, while the level of establishment by biocontrol agents in new geographical locations for this period was between 20 and 55 % (Gurr & Wratten, 1999).

Caltagirone (1981) reviewed several successful cases of insect biological control agents used internationally. The European winter moth *Operophtera brumata* L. (Geometridae), is a pest of oak woodlands and a threat to that sector of commercial forestry in North America. Successful control of the moth was obtained from a tachinid (*Cyzenis albicans* Fall.) and an ichneumonid (*Agrypon flaveolatum*). The programme to find, test and release suitable biocontrol agents cost $660,000. Control of this pest is estimated to have saved the Canadian economy the potential loss of $12 million in revenue (Embree, 1971). In another case the rhodesgrass mealybug, *Antonina graminis* Maskell, was successfully controlled by the encyrtid parasitoid, *Neodusmetia sangwani*, after a method of aerial dispersal of the apterous female wasps was devised. This programme is estimated to have increased grassland productivity and benefited the Texas economy by $177 million per annum (Dean *et al.*, 1979). The olive scale, *Parlatoria oleae* (Colvee), which in severe outbreaks can destroy olive crops, was controlled to acceptable levels for economic sustainability by the parasitoids *Aphytis maculicornis* (Masi) and *Coccophagoides utilis* Doutt (Huffaker & Kennett, 1966). The predatory mite, *Phytoseiulus persimilis* Athias-Henriot, controls the two-spotted mite (*Tetranychus urticae* Koch) a greenhouse pest, to levels of damage which are economically negligible (Hussey & Bravenboer, 1971). Insecticide resistance in pests can make some form of biocontrol the only viable method of control. When the walnut aphid, *Chromaphis juglandicola* (Kalt), became resistant to some insecticides, it was brought under control by using ecotypes of the parasitoid *Trioxys pallidus* (Haliday) climatically matched to regions of western USA (Frazer & van den Bosch, 1973).

Successful biocontrol programmes in New Zealand

The introduction of entomophagous biological agents to New Zealand began in 1874 when *Coccinella undecimpunctata* L.(Coleoptera: Coccinellidae) was imported to control aphids. Few other organisms were released until an initiative began to find methods for controlling weed and insect pests in the 1920s. Between 1874 and 1991 two-hundred and forty new organisms have been introduced to New Zealand for biocontrol purposes. However, the establishment rate has been low with only 75 species (31 %) successfully establishing in New Zealand (Cameron *et al.*, 1993). The establishment rate improved in the 1980s as more emphasis was placed on choosing species more climatically suited to New Zealand conditions, more rigorous release procedures were adopted, and the biology and ecology of biocontrol agents, their host organisms and the communities into which they were released, were better understood.

Of the new species successfully established in New Zealand, several have achieved desired control of the target pest, usually with no additional control required. In pastoral systems two species of clover casebearer, *Coleophora frischella* L. and *Coleophora spissicornis* Haworth (Lepidoptera: Coleophoridae), cause damage to clover seed production. Two parasitoids, a braconid *Bracon variegator* Nees and a eulophid *Chrysonotomyia trifolii* Erdos, successfully reduced *Coleophora* species numbers in clover crops to below economically-damaging levels (Pearson, 1989). The control of the cosmopolitan army worm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae), a pest of grain crops and pasture, was achieved after the introduction of the braconid larval parasitoid *Apanteles ruficrus* (Haliday) = *Dolichogenidea ruficrus* from Pakistan (Hill & Allan, 1989). It is estimated that the increased productivity following the successful control of this pest has benefited the New Zealand economy by between $4.5 and $10 million annually (Hill, 1977; Mohyuddin & Shah, 1977). The Argentine stem weevil, *Listronotus bonariensis* (Kuschel), is estimated to cost $165 million in lost production in New Zealand pastoral systems (G.Bartram, verbal paper, National Pest Summit, Palmerston North, 1999). Several ecotypes of *Microctonus hyperodae* Loan (Hymenoptera: Braconidae) were imported from South America to control *L. bonariensis*, and initial surveys indicated winter parasitism at 40-50 % and summer parasitism levels between 70-80 % (Goldson *et al.*, 1994).

In the horticultural sector there are three examples where biocontrol agents have controlled pests to levels below economic damage. The cottony cushion scale, *I. purchasi*, a pest of ornamental and citrus trees, was recorded as causing defoliation and fruit loss in severe outbreaks. *Icerya purchasi* is no longer regarded as an important pest because of the control achieved by the self-introduced coccinellid *R. cardinalis* and the introduced species *Cryptochetum iceryae* (Williston) (Diptera: Agromyzidae) (Morales & Bain, 1989a). The woolly apple aphid, *Eriosoma lanigerum* (Hausmann), is a serious pest of apple trees in New Zealand orchards, infests fruit, and damages woody tissue and roots. Only one parasitoid, *Aphelinus mali* (Haldeman) (Hymenoptera: Aphelinidae) was imported to control the aphid. A large release programme was undertaken in the 1920s with ecotypes of *A. mali* imported from several Australian locations and the USA. Where insecticide use is limited *A. mali* successfully controls *E. lanigerum* numbers (Walker, 1989). The damage to pome and stone fruit trees by the European red mite, *Panonychus ulmi* (Koch), was exacerbated by the use of DDT sprays in the 1950s which targeted lepidopterous pests and inadvertently reduced the natural enemies of the mite (Collyer, 1964). Maintenance of *P. ulmi* populations at low levels in orchards is achieved when insecticide use is limited allowing populations of the self-introduced predatory mite *Typlodromus pyri* Scheuten to survive (Walker *et al.*, 1989). Maintenance of natural enemy populations, where insecticide control regimes were used, was also a problem in control attempts of the two-spotted mite, *Tetranychus urticae* Koch, a serious pest of field and greenhouse crops. Significant control was achieved when the predatory mite *Phytoseiulus persimilis* (Athias-Henriot), which has developed resistance to a number of pesticides (McMurty *et al.*, 1978), was imported from England and later France. Development of integrated pest management programmes, including limited insecticide use and insecticide resistant *P. persimilis*, provide the required level of control of *T. urticae* (Thomas & Walker, 1989).

Several insect pests have threatened forestry production in New Zealand, biological control programmes have been aimed at ten of these pest species and are reviewed in Cameron *et al.* (1989). Damage by the gum tree weevil, *Gonipterus scutellatus* (Gyllenhal), can impair the growth of eucalyptus trees. This Australian pest was dramatically reduced in numbers, with reports of 70-80 % parasitism of weevil eggs, after the release of a mymarid wasp (*Anaphes nitens* Girault = *Anaphoidea nitens*) in the 1930s (Nuttall, 1989a). Another eucalyptus pest,

the gum tree scale (*Eriococcus coriaceus* Maskell), was noted to kill some commercial gum varieties in serious outbreaks during the early 1900s. From Australian reports on the parasitoids and predators known to attack *E. coriaceus*, several biocontrol agents were selected for importation and release. Of these species, the coccinellid *Rhyzobius ventralis* (Erichson), was successfully established and had a significant impact on *E. coriaceus* numbers. With the periodic redistribution of the coccinellid to locations with outbreaks and the use of eucalypt cultivars that are less susceptible to *E. coriaceus* attack, the scale is no longer an economically significant pest in New Zealand (Morales & Bain, 1989b).

The oak leafminer, *Phyllonorycter messaniella* (Zeller) (= *Lithocelletis messaniella)* (Lepidoptera: Gracillariidae) invaded New Zealand in the 1950s and was found to defoliate many ornamental species as well as oaks, such as native *Nothofagus* spp. and commercial apple and feijoa varieties (Wise, 1953; Wise, 1958), with some potentially serious economic consequences. Two parasitoids, *Apanteles circumscriptus* Nees (Braconidae) and *Achrysocharoides splendens* Delucchi (Eulophidae), were introduced from Europe and Canada. The parasitoids maintain *P. messaniella* populations at extremely low levels and this biocontrol programme is regarded as one of the most effective carried out in New Zealand (Thomas & Hill, 1989).

One of the most serious insect threats to commercial *Pinus radiata* Don production in New Zealand came from the sirex wood wasp, *Sirex noctilio* F. (Hymenoptera: Siricidae). Estimates in the late 1940s indicated that *S. noctilio* had killed approximately a third of the 120,000 hectares of pine grown on the central plateau of the North Island (Gilmour, 1965). Populations of *S. noctilio* become high when oviposition sites are increased by the non-removal of windthrown trees and when trees are stressed by drought. The wasp also indirectly causes tree death by spreading a symbiotic fungus during oviposition (Emberson, 1984). A suite of parasitoids from the families Ibaliidae and Ichneumonidae were introduced to attack *S. noctilio* and provided parasitism pressure of 25-35 %. However, the most effective control is thought to have come from an accidentally introduced nematode, *Deladenus siridicola* Bedding, which at times attacks the female gonads of up to 90 % of females in some populations (Zondag, 1975). A combination of cultural control practices, biocontrol and the accidentally introduced nematode now minimise *S. noctilio*-induced tree death (Nuttall, 1989b).

Justification for biological control use and alternatives

Successful biocontrol strategies have been implemented against pests of agriculture, horticulture, natural ecosystems and disease-carrying organisms (DeBach, 1974; Clausen, 1978; Waterhouse & Norris, 1987), with benefits to public health, the environment, increased and sustainable food production, and a reduction in chemical residues.

The use of biological control agents to control pests has been, and when non-target impacts are limited, still is regarded as a safe and more cost effective alternative to the use of chemicals to control pests. The non-target effects of pesticides on the environment have been well documented (Pimentel *et al.*, 1984). The major concerns regarding pesticide use are that they are not target specific and so eliminate both pest and beneficial species; their effectiveness maybe short-term as pesticide resistance has been demonstrated in many insect pest species; they can cause harm to public health; they can cause local extinctions of beneficial species; and they take time to decompose and some are present in the environment for extended periods. However, some authors maintain that when deleterious effects of vertebrate and invertebrate biocontrol agents occur they are more serious than those of chemical pesticides, because establishment of biocontrol agents is irreversible, chemicals do not genetically mutate, nor do they disperse as readily from the location at which they were applied (Howarth, 1991).

The use of biological control agents in native habitats can also be justified when pests attack fauna or flora of conservation value, particularly when invasive pests are more likely to devastate a community than non-target effects of biocontrol agents (Howarth, 1991; Simberloff, 1992). In New Zealand the vine, *Clematis vitalba* L., has established in native lowland forests throughout the North Island (Harman *et al.*, 1996). The vine can grow three metres per year and wind disperses seed rapidly (R.Hill., pers.comm. 1994). The vine forms a mat over the canopy trees, the weight of which can collapse trees and, by reducing light at lower forest levels, inhibit forest regeneration. This indirectly affects entire forest communities. Chemical control and manual removal of the vine are unfeasible because of the huge cost, inaccessibility of infestations, and non specificity of chemical application. For these reasons, several years of host range testing of candidate biocontrol agents have been conducted to ensure native *Clematis* species are not attacked. Recently this work has culminated in the release of *Phytomyza vitalbae* an agromyzid leaf-miner indigenous to Germany, a fungus,

Phoma clematidina Thum (Sphaeropsidales: Sphaeropsidaceae), and a sawfly, *Monophadnus spinolae* Klug (Hymenoptera: Tenthredinidae), from Switzerland.

Establishment of exotic pests and benefits of biocontrol programmes to New Zealand

New Zealand's economy is dependent on export revenue from agricultural and horticultural primary production (Anon, 1998; Halsted, 1988). The above examples demonstrate the serious threat to both the economy and the environment posed by exotic arthropods.

The consequences for biological diversity of deliberate and accidental introduction of exotic species to new geographical locations was reviewed by Vitousek *et al.*, (1997). Soule (1990) also outlined the increasing risks to biological diversity and public health posed by the establishment of exotic species. Since Cameron *et al.*, (1989) reviewed the history of New Zealand's biological control of pest species, further biological pests have colonised New Zealand and have been recognised as potential or actual threats to the environment, forestry, horticulture, agriculture or public health. Charles (1998) estimated that fruit crop pests, presently classified as non-critical, are colonising New Zealand at a rate of seven species per decade. A recent estimate indicates that vertebrate and invertebrate pests cost the New Zealand economy $840 million per annum in prevention, control and loss of production (G. Bartram, verbal paper, National Pest Summit, Palmerston North, 1999). Several insect species have invaded New Zealand in recent years, including the following. The willow sawfly (*Nematus oligospilus* Forster) which may threatens willow and some poplar species used for erosion control in riparian zones. The white-spotted tussock moth (*Orgyia thyellina*) which had the potential to attack native and exotic forestry, but was eradicated from Auckland using *Bacillus thuringiensis* variety *kurstaki* (Hutching, 1996). The Asian tiger mosquito, was contained near Auckland and Wellington ports and eradicated using insecticide. The Australian mosquito, *Aedes camptorynchus,* which can potentially carry disease such as the Ross River virus, is being eradicated using *B. thuringiensis* variety *israelensis*. The clover root weevil (*Sitona lepidus*) which could have serious consequences for pastoral farming by directly reducing the proportion of clover within pastures and by indirectly lowering soil fertility, has become established in the North Island. Many of these pests are candidates for control by the importation of insect biocontrol organisms or fungal or bacterial pathogens.

The economic consequences of exotic pests establishing in New Zealand are manifest as a loss of productivity and/or increased production costs (i.e., pest control costs) for primary producers and as possible trade restrictions. Some competitive advantage may be conferred to New Zealand produce by the declining use of chemicals and introduction of integrated pest management strategies for several fruit crops, such as the Kiwi Green initiative used for kiwifruit production. Therefore, reliance on natural enemies to control insect and plant pests will increase either by improving the management of the existing natural enemy complexes or introducing further biological control agents where natural enemies of the pest species are depauperate (Charles, 1998).

Concurrently, increasing recognition of the level of endemism and value of New Zealand's native insect fauna makes the conservation and protection of these species increasingly important (Roberts, 1986; Dugdale, 1988; Gibbs, 1990). The deliberate and accidental introduction of exotic species may threaten native flora and fauna. In some instances, the most effective and least costly option to combat exotic pests is to use insect biocontrol agents. For example, the invasive vine *C. vitalba* was introduced to New Zealand as an ornamental plant and used as a rootstock for cultivated *Clematis*. *Clematis vitalba* has invaded many areas of native vegetation including national parks, and chemical control is not feasible because of its cost and non-selectiveness. A biological control programme has now been implemented to control this vine (Harman, *et al*., 1996).

However, some of these same biological control agents imported to control economic and environmental pests may also become pests themselves by having direct or indirect impacts on native fauna and flora. Therefore, all care must be taken to establish that insect biocontrol agents are rigorously tested prior to their introduction, to ensure that the potential benefits of this method exceed any potential risk of negative impacts.

Recognition of non-target effects

Greater potential for biological control agents to have deleterious effects on non-target fauna began to be recognised in the early 1980s (Howarth, 1983; Pimentel *et al*., 1984; Harris, 1988) and has been debated extensively (Howarth, 1983; Samways, 1988; Howarth, 1991; Simberloff, 1992; Hokkanen & Lynch, 1995; Secord & Kareiva, 1996; Simberloff & Stiling, 1996a; Simberloff & Stiling, 1996b; Sands, 1997; Barratt *et al*., in press b). Also at this time,

the intrinsic value of native insect fauna and the need to conserve these species was recognised (Pyle *et al.*, 1981). The lack of direct causative examples of insect biocontrol agents causing extinctions is believed by some to reinforce the opinion that biological control is a safe practice (Lai, 1988; Funasaki *et al.*, 1988; Messing, 1992; Carruthers & Onsager, 1993) and that current safety testing methods minimise risks (DeLoach, 1991).

Examples of extinction among native species associated with the introduction of exotic species for biological control has been most clearly demonstrated where generalist vertebrate or molluscan predators have been used (Howarth, 1991). It is difficult retrospectively to attribute any invertebrate extinctions to specific biological control agents, although some authors maintain that this is a result of a dearth of post-release studies (Simberloff, 1992). In the past, the dispersal of biocontrol agents to native habitats and non-target impacts have often been discovered serendipitously as a result other work in an environment (Early, 1995; Murray *et al.*, 1988). An example of this was the long-term study of the genetic variability among *Partula* spp. land snail populations isolated by valleys on the Pacific Island of Moorea. The extinction of seven *Partula* species coincided with the introduction of the predacious land snail (*Euglandina rosea* Ferussac), targeted at the giant African land snail (*Achatina fulica* Bowdich), an exotic crop pest (Murray *et al.*, 1988).

Non-target effects

While it has been difficult to do more than form an associative relationship between biocontrol agents and the extinction of non-target species, other detrimental effects have been clearly demonstrated. Non-target effects were defined by Barratt *et al.*, (in press a) as "any measurable effect on non-target species resulting from the introduction of an exotic organism", however this definition could also include effects that are indirectly beneficial to non-target species. Undesirable effects include direct parasitism or predation of non-target species, competition for resources with other beneficial species or inducing habitat changes that affect native fauna (McEvoy 1996; Secord & Kareiva, 1996).

Several classes of non-target effect as a result of the practice of biological control have been recognised. The following are types of non-target effect presently recognised or thought possible to occur when biological control is practiced. They are mainly examples of entomophagous biocontrol and, where possible, New Zealand cases.

Non-target attack of hosts. The attack of non-target hosts by an introduced predator or parasitoid is probably the most easily demonstrated negative impact of biocontrol agents. This is of serious concern when the host or prey are rare natives, beneficial species or other biocontrol agents. In New Zealand, examples of non-target hosts include the native red admiral butterfly *Bassaris gonerilla* Fabricius attacked by the parasitoid of the white butterfly *Pieris rapae* L. (Barratt *et al.*, in press a), several species of native Lepidoptera are attacked by the leafroller parasitoid *Trigonospila brevifacies* (Hardy) (Green, 1984; Munro, Chapter 3), and the weevil *Rhinocyllus conicus* (Froelich) attacked by the Sitona weevil parasitoid *Microctonus aethiopoides* Loan (Ferguson *et al.*, 1994). This is an instance of one biocontrol agent attacking another, *R. conicus* was introduced as a biocontrol agent for nodding thistle *Carduus nutans* L. (Jessep, 1989).

Habitat invasion. The ability of biocontrol agents to disperse and invade non-target habitats can bring them into contact with new hosts and competition with species of the same trophic level from which they were formerly ecologically separated. It was assumed that it was unlikely that the Argentine stem weevil parasitoid, *M. hyperodae,* could colonise alpine tussock lands in New Zealand and come into contact with native weevils, but records indicate that the parasitoid could be transported to these areas by its parasitised target host (Barratt *et al.*, in press a). *Trigonospila brevifacies* has also invaded native forests in the North Island and dispersed to offshore islands from the orchard areas into which it was released (Early, 1995; Munro, 1998a; Munro, 1998b). The degree of impact the new organism has on hosts in a new habitat may be restricted by the invasibility of the habitat which could provide host refuges.

Biocontrol agents becoming pests. Biocontrol agents can also become pests themselves (Pimentel *et al.,* 1984), as demonstrated in Australia, by the introduction of the cane toad *Bufo marinus* L. (Freeland, 1986) and in Uganda, where the hemipteran *Teleonemia scrupulosa* released to attack Lantana vine shifted to sesame crops. However, *T. scrupulosa* was unable to reproduce on sesame, limiting its impact on the crop (Greathead, 1971). Recently the leafmining lepidopteran *Dialectica scalariella* Zeller, introduced to control Patterson's curse, *Echium plantagineum* L., in Australia has invaded New Zealand and is damaging ornamental echium in Auckland, Te Puke, Nelson and Christchurch (J.S. Dugdale, Landcare Research, pers.comm. 1998). Interestingly the dispersal of *D. scalariella* to New

Zealand could also have a beneficial outcome, as *Echium vulgare* L. is a significant introduced weed in Otago and the leafminer may become a useful control agent for this weed (C.H. Wearing, pers. comm. 1999).

Adaptation. There is a risk that adaptation to new hosts or climatic conditions will occur some time after release, depending on the degree of genetic plasticity. The propensity for this to occur has been demonstrated by neoclassical biocontrol which uses new associations between host and biocontrol agents (Hokkanen & Pimentel, 1989). However in these instances the attack of hosts with which the biocontrol agent had no shared evolutionary history was intended. Adaptation to new hosts may be less likely when monophagous or oligophagous species are chosen for release in classical biocontrol programmes.

Competition. Competition for hosts between native species and introduced biocontrol agents may lead to competitive displacement. *Trigonospila brevifacies,* in New Zealand, is known to host-share with several native Hymenoptera for hosts, but the effect this has on the population dynamics of the native fauna is unknown (Munro, Chapter 4). Competitive displacement has been shown between exotic biocontrol agents (Murdoch *et al.*, 1996) and instances where native parasitoids are thought to have been displaced by introduced species are discussed by Bennett (1993).

Contagen vectors. Biocontrol agents can also affect non-target host populations by acting as vectors of mutualistic contagens. The parasitic wasp *M. aethiopoides* was found to cause sterility in its target and one non-target weevil species and it is suspected that a contagen is transmitted to its hosts via the female wasp's ovipositor (Barratt *et al.*, in press b).

Environmental effects. Biocontrol agents may also alter environments. It has been speculated that a reduction in native weevil density by *M. aethiopoides* parasitism may increase the prevalence of the pasture weed *Hieracium* in South Island pastures (Barratt *et al.*, in press b). It has also been hypothesised that the *Myxoma* virus, illegally introduced to control rabbits in Great Britain, led to the extinction of the large blue butterfly *Maculina arion* L. when reduced rabbit grazing resulted in the loss of suitable habitat for the butterfly (Howarth, 1991).

Community effects. Possible indirect community effects are difficult to quantify, but when biocontrol agents become keystone species within a community they have the potential to affect a greater number of species. Simberloff & Stiling (1996b) define a keystone species as

"any species that affects directly or indirectly most species in the community, these effects often being out of proportion to the abundance or biomass of the keystone species itself".

The practice of biological control can indirectly lead to conflict among interest groups that can have serious consequences for both native and beneficial organisms. Two Australasian cases, the introduction of insect biocontrol agents for Patterson's curse in Australia and the RCD virus to control rabbits in New Zealand resulted in conflict. Patterson's curse became a serious plant pest in pastoral farmland areas of Australia. When biological control was proposed for this plant, it was opposed in courts of law by apiarists who regarded *E. plantagineum* pollen as valuable in some regions. The matter was eventually resolved and insect agents introduced (Delfosse, 1988). In New Zealand, rabbit populations in the South Island were reducing the profitability of high country farming. Risk assessments were being conducted to determine whether the calici virus RCD would be introduced to control the rabbits. The major concerns were the mutability of the calici virus family and the risk that rabbit predators such as mustelids and wild cats might switch to rare birds and other native fauna if rabbit numbers declined. In 1997 RCD was illegally imported and released in the South Island. In anticipation of objections to the proposed introduction of biocontrol agents to control gorse *Ulex europaeus* L. in New Zealand agricultural and conservation lands, interest groups were asked to make submissions. In particular bee keepers feared the loss of valuable autumn honey sources. Consideration of New Zealand apiarists concerns and economic assessment of potential losses were made prior to the introduction of biocontrol agents for gorse (Syrett *et al.*, 1985; Hill, 1986).

Routine host range testing: a procedure to reduce non-target effects

It is unarguable that biodiversity is threatened in many regions of the world by cultivation of, or resource extraction in, natural areas, or by invasion of new organisms and this requires serious consideration (Wilson, 1985; Samways, 1988; Soule, 1990; Vitousek *et al.*, 1997). Therefore, it is imperative that introductions of exotic organisms for biological control do not contribute to further reductions in biodiversity. Instances of vertebrate and molluscan biocontrol agents causing local extinctions or reducing the abundance of non-target species are well documented. There are some anecdotal examples where entomophagous biocontrol agents are implicated as causing regional extinctions of species, though quantitative studies are lacking. The tachinid

B. remota is attributed with causing the extinction of the coconut moth *L. iridescens*, the intended target of the biocontrol programme, and another zygaeid, *Heteropan dolens*, became locally extinct (Rao *et al.*, 1971; Howarth, 1991). There are no known cases of phytophagous biocontrol agents causing extinctions of non-target plant species (Groves, 1989; DeLoach, 1991). Host range testing of candidates for weed biological control has been quite rigorous to reduce the risk of attack to economically important crops (Simberloff & Stiling, 1996b). However, insect biocontrol agents introduced to control weeds have been known to attack closely related non-target plants particularly when they disperse away from their intended location. The cactus moth, *Cactoblastis cactorum*, which was introduced to the Lesser Antilles islands to control *Opuntia* species, has now dispersed to the southern USA and threatens a rare cactus species (Simberloff, 1992). Therefore, it is undeniable that the practice of biological control can have negative impacts on non-target fauna and it is the degree of these impacts that is yet to be ascertained.

Improved methods for testing the potential host range of entomophagous arthropods may reduce the likelihood of negative effects. Historically, host range testing of a candidate for biocontrol was limited to three criteria; could the candidate species successfully reproduce on the target host; that the candidate did not attack other natural enemies; and did not attack biocontrol agents of other pest species (Van Driesche & Hoddle, 1997). Formerly, polyphagy in entomophagous biocontrols had been considered a desirable attribute for improving the low rates of establishment among released species. The present aim is to find monophagous or oligophagous species which will provide adequate control of a target species.

The current debate regarding pre-release host range testing for biocontrol agents centres on its necessity. It is still maintained by some that there are no quantitative and few anecdotal instances of non-target consequences when arthropod biocontrol agents have been used. Others view mandatory host range testing as an impediment to future introductions of exotic species preferring testing to be limited to rare species (Hopper, 1995). One complication with this argument is that the limited taxonomic knowledge of fauna in some countries, including New Zealand, makes it difficult to identify species that may be at risk (Barratt *et al.*, in press b). It is also argued that the cost of extensively testing a range of potential hosts may prohibit the use of future biocontrol programmes (Van Driesche & Hoddle, 1997). Van Driesche & Hoddle (1997) also cite data from Australia showing that when mandatory host

range testing of entomophagous agents was introduced costs per programme increased by 80 % and the number of programmes undertaken decreased by 30 %. Increased pre-release testing could provide the benefits of choosing biocontrol agents that are more likely to establish and provide effective pest control by ensuring target hosts are more preferred than the non-target host and limit the negative effects on non-target fauna (Goldson, *et al.*, 1992). However, when attempts have been made to correlate characteristics thought to indicate success with post release data, it was found that optimal candidates were no more successful (Van Driesche & Hoddle, 1997).

One of the major arguments against accepting or rejecting biocontrol candidates based on present host range testing methods is that cage tests can overestimate the number of species likely to be attacked in the field (Balciunas *et al.*, 1996). Alternatively, host range testing may not be able to predict if adaptation to new hosts will occur over time. Some post-release studies have been conducted in recent years to determine if pre-release host range testing is a good predictor of the actual field host range (Nafus, 1993; Balciunas *et al.*, 1996; Barratt *et al.*, 1997; Barratt *et al.*, 1998; Barratt *et al.*, in press a). Pre-release work on *M. hyperodae* in New Zealand has proven to be an accurate predictor of the host range this braconid has acquired in the field (Barratt *et al.*, in press a). Further quantitative studies are required, particularly because the limited records held in archives do not give an accurate measure of parasitism or predation as a mortality factor for non-target hosts. For example, records of a parasitoid attacking a certain host species does not necessarily mean that it is having an impact on that host's population. More such studies are recommended to improve the practice of biological control (Van Driesche & Hoddle, 1997; Barratt *et al.*, in press a; Barratt *et al.*, in press b). It has also been suggested that as well as more precise data on biocontrol agents, further ecological, taxonomic and natural history data of target species, and phylogenetically or ecologically similar native species are necessary. Again the work on *M. hyperodae* has illustrated the value of this point. Although the predicted host range is similar to that in the field it was not anticipated that the target weevil could disperse to alpine regions nor that it could carry the *M. hyperodae* there. It was assumed that the parasitoid would remain ecologically separated from native alpine Curculionidae (Barratt *et al.*, in press a).

Van Driesche and Hoddle (1997) made recommendations on how much host range testing should be conducted in the future, with differing proposals for continental and island

states. They recommended an increase in testing for all entomophagous candidate biocontrol agents. Testing on continents, should be carried out to determine if candidate control agents are polyphagous, if they attack species of economic value (such as beneficial insects and other biocontrol agents) and if they can reproduce successfully on endangered species under laboratory conditions. For islands, increased levels of host range testing are proposed because of the higher level of endemism species with smaller geographical ranges and the greater feasibility of testing the smaller numbers of potential non-target hosts in a genus or family.

International requirements for host specificity testing

Extensive host range testing prior to the release of entomophagous biocontrol agents is executed in few countries (Van Driesche & Hoddle, 1997). A Code of Conduct for the Importation and Release of Biological Control Agents was ratified by the FAO council in 1995. The code furnishes guidelines for the process by which biocontrol agents are introduced, and practices that prevent negative environmental impacts are recommended (Schultern, 1997). Simberloff & Stiling (1996b) briefly review the procedure for introducing biological control agents to the USA. No specific state or congressional law requires host specificity testing of biocontrol agents prior to release, but all introductions must be approved by the Biological Assessment and Taxonomic Support group. In Australia, pre-release testing is mandatory and in New Zealand it is accepted practice to determine in quarantine the host range of candidate biocontrol agents using choice and/or no-choice methods.

In 1984 the Australian federal government passed the Australian Biological Control Act (1984). This act requires practitioners of biological control to demonstrate that the candidate species poses no significant harm to any person or to the environment. With the introduction of the Biosecurity Act (1993) and the Hazardous Substances and New Organisms Act (1996), New Zealand legislation currently exceeds the proposals of the FAO code (Barratt *et al.*, in press a). Under the HSNO Act, bodies introducing biocontrol agents must avoid; "harmful effects to New Zealand's genetic diversity"; "deterioration of natural habitat"; "displacement of native species in natural habitats", and environmental, economic and cultural values must also be considered.

Any legislation governing the introduction of biological control agents must provide ways to ensure their safety while maintaining the ability to use biocontrol as an effective non-

chemical control strategy for entomophagous and phytophagous pests in commercial and conservation areas.

Future challenges for biological control

The major challenge facing practitioners of biological control at present and in the future is to improve the process of introducing low risk, effective biological control agents by the development of better pre-release methodologies which more precisely predict the final outcome of release programmes. These include accurately predicting field host ranges of biocontrol agents, identifying habitat preferences, studying the ecology of both the pest and candidate control species more thoroughly, and post-release monitoring of the introduced agents. These data can be used to further improve the process of biocontrol selection and provide the information necessary for decision making by agencies which sanction the importation and release of new organisms. Gathering data from instances where non-target effects of biological control agents are detected, and documenting this information, will aid the development of theory and reduce the risk from future biocontrol programmes (Caltagirone, 1981; Barratt, *et al.*, in press *a*).

The issue of what levels of non-target impacts are acceptable also needs to be addressed. Some negative impacts are probably inevitable and will be irreversible. Obviously the extinction or significant numerical reduction of a native or beneficial species is unacceptable, but isolated post-release attacks on non-target hosts in the field should not prohibit the use of certain biocontrol agents ?

Consideration of the tangible economic and environmental value of biological control organisms to control weeds and pests, must be weighed against the risk that serious unforeseen negative effects might occur or that restriction of biocontrol practices limits the methods available to combat the increasing number of invasive species accidentally dispersed worldwide by human activity.

Aims of the present study

The parasitoid *T. brevifacies* was introduced, to New Zealand, in the late 1960s from Australia to control the lightbrown apple moth (*Epiphyas postvittana* (Walker)) in fruit crops (Thomas, 1989). No pre-release study was made of *T. brevifacies* potential host range in New Zealand. It became apparent in the early 1980s that *T. brevifacies* attacked non-target native Lepidoptera in orchard and urban areas (Green, 1984; Roberts, 1986). What had not been determined was the range of species parasitised, the frequency and level of attack, and whether other fauna were being indirectly affected by *T. brevifacies.*

This thesis aims to make a comprehensive post-release study where the non-target impacts of the leafroller biocontrol agent *T. brevifacies*, on native lepidopteran fauna in New Zealand, are identified and quantified. Five aspects of *T. brevifacies* life history and ecology were chosen for study. The first aim was to determine the present distribution of *T. brevifacies* and *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae), a parasitoid of lepidopteran pupae introduced concurrently with *T. brevifacies*, in New Zealand. These data, with archival data of the parasitoids' distribution in Australia, were used to determine in which climatic zones the parasitoids had established and make predictions of which other areas of New Zealand could be successfully colonised in the future by *T. brevifacies* and *X. rhopaloceros.* Secondly, the host range, frequency of attack and level of parasitism exerted by *T. brevifacies* on non-target Lepidoptera in native forests was quantified. Other native fauna are also likely to be indirectly affected by *T. brevifacies* parasitism of non-target hosts. Thirdly, the native parasitoid guild was studied to determine which species *T. brevifacies* competed with for hosts and subsequently the level of these interactions was quantified. The fourth aim was to determine the reproductive capabilities and life history of *T. brevifacies* and from these data make predictions of its impact on non-target hosts. The final objective was to measure the distribution of *T. brevifacies* and its larval hosts within native forests. These patterns were then matched to actual levels of parasitism along edge to centre transects in forest patches. Then it was determined if parasitism differed between zones in native forest patches and if so, identify parasitoid free areas which could provide refuges for non-target hosts.

REFERENCES

Anonymous (1998) Agriculture and forest industries. In: *New Zealand Official Year Book 1997-98*, volume 103.

Balciunas, J.K., Burrows, D.W., Purcell, M.F. (1996) Comparison of the physiological and realized host-ranges of a biological control agent from Australia for the control of the exotic weed *Hydrilla verticillata. Biological Control* **7**: 148-158.

Barratt, B.I.P., Evans, A.A., Ferguson, C.M., Barker, G.M., McNeil, M.R., Phillips, C.B. (1997) Laboratory non-target host range of the introduced parasitoids *Microctonus aethiopoides* and *Microctonus hyperodae* (Hymenoptera: Braconidae) compared with field parasitism in New Zealand. *Environmental Entomology* **26**: 694-702.

Barratt, B.I.P., Evans, A.A., Ferguson, C.M., McNeil, M.R., Proffitt, J.R., Barker, G.M. (1998) Curculionoidea (Insecta: Coleoptera) as potential non-target hosts of the parasitoids *Microctonus aethiopoides* and *Microctonus hyperodae* (Hymenoptera: Braconidae). *New Zealand Journal of Zoology* **25**: 47-63.

Barratt, B.I.P., Goldson, S.L., Ferguson, C.M., Phillips, C.B., Hannah, D.J. (in press *a*) Predicting the risk from biological control agent introductions: a New Zealand approach. In: Biological Control for a Small Planet: nontarget effects of biological control introductions (Follett, P.A., Ed). Kluwer Academic Press.

Barratt, B.I.P., Ferguson, C.M., Evans, A.A. (in press b) Implications of the effects of introduced biological control agents on native and beneficial non-target species. In: *Balancing Nature: Assessing the Impact of Importing Exotic Biological Control Agents - an international perspective* (Purcell, M., Lockwood, J., Howarth, F., Eds). Thomas Say Publication Series.

Bartlett, B.R. (1978) Coccidae. In: *Introduced Parasites and Predators of Arthropod Pests and Weeds: a world review*, (Clausen, C.P., Ed). United States Department of Agriculture, Agricultural Research Service, Agricultural Handbook 480. pp: 132-136.

Bennett, F.D. (1993) Do introduced parasitoids displace native ones? *Florida Entomologist* **76**: 54-63.

Caltagirone, E.L. (1981) Landmark examples of classical biological control. *Annual Review of Entomology* **26**: 213-232.

Cameron, P.J., Hill, R.L., Valentine, E.W., Thomas, W.P. (1987) Invertebrates Imported into New Zealand for the Biological Control of Invertebrate Pests and Weeds, for Pollination and Dung Dispersal, from 1874 to 1985. *DSIR Bulletin*. pp 245: 255.

Cameron, P.J., Hill, R.L., Bain, J., Thomas, W.P. (1989) A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874-1987. Technical Communication, CAB International Institute of Biological Control 10, CAB International, Wallingford, UK.

Cameron, P.J., Hill, R.L., Bain, J., Thomas, W.P. (1993) Analysis of importations for biological control of insect pests and weeds in New Zealand. *Biocontrol Science and Technology* **3**: 387-404.

Carruthers, R.I., Onsager, J.A. (1993) Perspective on the use of exotic natural enemies for biological control of pest grasshoppers (Orthoptera: Acrididae). *Environmental Entomology* **22**: 885-903.

Charles, J.G. (1998) The settlement of fruit crop arthropod pests and their natural enemies in New Zealand: an historical guide to the future. *Biocontrol News and Information* **19**: 47-58.

Clausen, E.P. (1978) *Introduced Parasites and Predators of Arthropod Pests and Weeds: a world review*. United States Department of Agriculture, Agricultural Research Service, Agricultural Handbook 480.

Collyer, E. (1964) Phytophagous mites and their predators in New Zealand orchards. *New Zealand Journal of Agricultural Research* **7**: 551-568.

Dean, H.A., Schuster, M.F., Boling, J.C., Riherd, P.T., (1979) Complete biological control of *Antonina graminis* in Texas by *Neodusmetia sangwani* (A classical example). *Bulletin of the Entomological Society of America* **25**: 262-267.

DeBach, P. (1974) Biological Control by Natural Enemies. Cambridge University Press, London, UK.

DeBach, P., Rosen, D. (1991) Biological Control by Natural Enemies. Second edition. Cambridge University Press, Cambridge, UK.

DeLoach, C.J. (1991) Past successes and current prospects in biological control of weeds in the United States and Canada. *Natural Areas Journal* **11**: 129-142.

Delfosse, E.S. (1988) *Echium* appeal won by CSIRO. *News Bulletin of the Australian Entomological Society* **24**: 149-152.

Dugdale, J.S. (1988) Lepidoptera - annotated catalogue, and keys to family-group taxa. DSIR Science Information Publishing Centre, Wellington, New Zealand.

Early, J.W. (1995) Insects of the Aldermen Islands. *Tane* **35,** 1-14.

Emberson, R.M. (1984) Forest and Timber Insects. In: *New Zealand Pest and Beneficial Insects* (Scott, R.R., Ed). Lincoln University of Agriculture, Canterbury, New Zealand. pp 191-204.

Embree, D.G. (1971) The biological control of the winter moth in eastern Canada by introduced parasites. In: Biological Control (Huffaker, C.B., Ed). Plenum, New York, USA. pp 217-226.

Ferguson, C.M., Roberts, G.M., Barratt, B.I.P., Evans, A.A., Popay, A.J. (1994) The distribution of the parasitoid *Microctonus aethiopoides* (Hymenoptera: Braconidae) in southern South Island *Sitona discoideus* (Coleoptera: Curculionidae) populations. In: Proceedings of the 47th New Zealand Plant Protection Conference (Popay, A.J., Ed). New Zealand Plant Protection Society. pp 261-265.

Fox, K.J. (1974) Trans-oceanic dispersal of insects in New Zealand. *New Zealand Entomologist* **5,** 240-243.

Frazer, B.D., van den Bosch, R. (1973) Biological control of the walnut aphid in California: the interrelationships of the parasite and its host. *Environmental Entomology* **2**: 561-568.

Freeland, W.J. (1986) Invasion north successful conquest by the cane toad. *Australian Natural History* **22**: 69-72.

Funasaki, G.Y., Lai, P-Y., Nakahara, L.M., Beardsley, J.W., Ota, A.K. (1988) A review of biological control introductions in Hawaii: 1890 to 1985. *Proceedings of the Hawaii Entomological Society* **28**: 105-160.

Gibbs, G, W. (1990) The silent majority: a plea for the consideration of invertebrates in New Zealand island management. *In*: Ecological Restoration of New Zealand Islands (Townes, D.R., Daugherty, C.H., Atkinson, I.A.E., Eds). Department of Conservation, Wellington, New Zealand. pp 123-127.

Gilmour, J.W. (1965) The life cycle of the fungal symbiont of *Sirex noctilio*. *New Zealand Journal of Forestry* **10**: 80-89.

Goldson, S.L., McNeill, M.R., Phillips, C.B., Proffitt, J.R. (1992) Host specificity testing and the suitability of the parasitoid *Microctonus hyperodae* (Hymenoptera: Braconidae) as a biological control agent of *Listronotus bonariensis* (Coleoptera: Curculionidae) in New Zealand. *Entomophaga* **37**: 483-498

Goldson, S.L., Barker, G.M., Barratt, B.I.P. (1994) The establishment of an Argentine stem weevil parasitoid at its release sites. *Proceedings of the 47th New Zealand Plant Protection Conference*. pp 274-276.

Greathead, D.J. (1971) A review of Biological Control in the Ethiopian Region. CAB Technical Bulletin 5. Commonwealth Agricultural Bureau, Slough, UK.

Green, O. R. (1984) New Zealand host and locality records for an introduced tortricid parasite, *Trigonospila brevifacies* (Diptera: Tachinidae). *New Zealand Entomologist* **8**: 69-71.

Groves, R.H. (1989) Ecological control of invasive terrestrial plants. In: Biological invasions: a global perspective (Drake, J.A., Mooney, H.A., diCastri, F., Groves, R.H., Kruger, F.J., Rejmanek, M., Williamson, M., Eds). Wiley, Chichester UK. pp 437-461.

Gurr, G.M., Wratten, S.D. (1999) Integrated biological control: a proposal for enhancing success in biological control. *International Journal of Pest Management* **45**: 81-84.

Halsted, J.V. (1988) Export statistics. Fresh fruit leads horticultural exports. *The Orchardist of New Zealand* **61**: 34-37.

Harman, H.M., Syrett, P., Hill, R.L., Jessop, C.T. (1996) Arthropod introductions for biological control of weeds in New Zealand, 1929-1995. *New Zealand Entomologist* **19**: 71-80.

Harris, P. (1988) Environmental impact of weed-control insects. *Bioscience* **38**: 542-548.

Hill, M.G. (1977) Parasite helps control army caterpillar. *New Zealand Journal of Agriculture* **25**: 251-254.

Hill, M.G., Allan, D.J. (1989) *Mythimna separata*, cosmopolitan armyworm (Lepidoptera: Noctuidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 107-109.

Hill, R.L. (1986) Biological control of gorse: implications for the natural environment and primary production. *Entomology Division, DSIR*, **Report 6**. pp: 130.

Hokkanen, H.M.T., Pimentel, D. (1989) New associations in biological control: theory and practice. *Canadian Entomologist* **121**: 829-840.

Hokkanen, H.M.T., Lynch, J.M. (1995) Biological control: benefits and risks. Cambridge University Press, Cambridge, UK.

Hopper, K.R. (1995) Potential impacts on threatened and endangered insect species in the United States from introductions of parasitic Hymenoptera for the control of insect pests. In: *Biological Control: Benefits and Risks* (Hokkanen, H.M.T., Lynch, J.M., Eds). Cambridge University Press, Cambridge, UK. pp 64-74.

Howarth, F. G. (1983) Classical biological control: panacea or Pandora's box. *Proceedings of the Hawaiian Entomological Society* **24**: 239-244.

Howarth, F. G. (1991) Environmental impacts of classical biological control. *Annual Review of Entomology* **36**: 485-509.

Huffaker, C.B., Kennett, C.E. (1966) Biological control of *Parlatoria oleae* through compensatory action of two introduced parasites. *Hilgardia* **37**: 283-335.

Hussey, N.W., Bravenboer, L. (1971) Control of pests in glass-house culture by the introduction of natural enemies. In: *Biological Control*. (Huffaker, C.B., Ed). Plenum, New York, USA. pp 195-216.

Hutching, G. (1996) Soft furry and a danger to native forests: white-spotted tussock moth. *Forest and Bird* August: 14-19.

Jessep, C.T. (1989) *Carduus nutans*, nodding thistle (Asteraceae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 339-342.

Lai, P-Y. (1988) Biological control: a positive point of view. *Proceedings of the Hawaii Entomological Society* **28**: 179-190.

McEvoy, P.B. (1996) Host specificity and biological pest control. *BioScience* **46**: 401-405.

McMurtry, J.A., Oatman, E.R., Phillips, D.A., Wood, C.W. (1978) Establishing *Phytoseiulus persimilis* (Acari: Phytoseiidae) in southern California. *Entomophaga* **23**: 175-179.

Messing, R.H. (1992) Biological control in island ecosystems: Cornerstone of sustainable agriculture or threat to biological diversity. *Pacific Science* **46**: 387-388.

Mohyuddin, A.I., Shah, S. (1977) Biological control of *Mythimna separata* (Lep: Noctuidae) in New Zealand and its bearing on biological control strategy. *Entomophaga* **22**: 331-333.

Moon, R.D. (1980) Biological control through interspecific competition. *Environmental Entomology* **9:** 723-728.

Morales, C.F., Bain, J. (1989a) *Icerya purchasi*, cottony cushion scale (Homoptera: Margarodidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 207-211.

Morales, C.F., Bain, J. (1989b) *Eriococcus coriaceus*, gum tree scale (Homoptera: Eriococcidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds).CAB International, Wallingford, U.K. pp 263-266.

Munro, V.M.W, (1998*a*) A record of the releases and recoveries of the Australian parasitoids, *Xanthopimpla rhopaloceros* (Ichneumonidae) Krieger and *Trigonospila brevifacies* (Hardy) (Tachinidae), introduced to New Zealand for leafroller control. *New Zealand Entomologist* **21**: 81-91

Munro, V.M.W, (1998*b*) A retrospective analysis of the establishment and dispersal of the introduced Australian parasitoids *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) within New Zealand. *Biocontrol, Science and Technology* **8**: 559-571.

Murdoch, W.W., Briggs, C.J., Nisbet, R.M. (1996) Competitive displacement and biological control in parasitoids: a model. *The American Naturalist* **148**: 807-826.

Murray, J., Murray, E., Johnson, M.S., Clarke, B. (1988) The extinction of *Partula* on Moorea. *Pacific Science* **42**: 150-153.

Nafus, D.M. (1993) Movement of introduced biological control agents onto nontarget butterflies, *Hypolimnas* spp. (Lepidoptera: Nymphalidae). *Environmental Entomology*, **22**: 265-272.

Nuttall, M.J. (1989a) *Gonipterus scutellatus*, gum tree weevil (Coleoptera: Curculionidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 267-269.

Nuttall, M.J. (1989b) *Sirex noctilio*, sirex wood wasp (Hymenoptera: Siricidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 299-306.

Pearson, W.D. (1989) *Coleophora frischella*, whitetipped clover casebearer, *C. spissicornis*, banded clover casebearer (Lepidoptera: Coleophoridae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 73-84.

Pimentel, D., Glenister, C., Fast, S., Gallahan, D. (1984) Environmental risks of biological pest controls. *Oikos* **42**: 283-290.

Pyle, R., Bentzien, M., Opler, P. (1981) Insect conservation. *Annual Review of Entomology* **26**: 233-258.

Rao, V.P., Ghani, M.A., Sankaren, T., Mathur, K.C. (1971) A Review of the Biological Control of Insects and Other Pests in South-East Asia and the Pacific Regions. CAB, London, UK.

Roberts, L. I. N. (1986) The practice of biological control - implications for conservation, science and community. *The Weta* **9**: 76-84.

Samways, M.J. (1988) Classical biological control and insect conservation: are they compatible? *Environmental Conservation* **15**: 349-354

Sands, D.P.A. (1997) The safety of biological control agents: assessing their impact on beneficial and other non-target hosts. *Memoirs of the Museum of Victoria* **56**: 611-615.

Schultern, G.G.M. (1997) The FAO code of conduct for the import and release of exotic biological controls. In: *EPPO/CABI workshop on safety and efficacy of biological control in Europe* (Smith, I.M., Ed). Blackwell Science Ltd, Oxford, UK. pp 29-36.

Secord, D., Kareiva, P. (1996) Perils and pitfalls in the host specificity paradigm. *Bioscience* **46**: 448-453.

Simberloff, D. (1992) Conservation of pristine habitats and unintended effects of biological control. In: *Selection Criteria and Ecological Consequences of Importing Natural Enemies* (Kauffman, W.C., Nechols, J.E., Eds) Entomological Society of America, Lanham, USA. pp 103-117.

Simberloff, D., Stiling, P. (1996a) How risky is biological control ? *Ecology* **77**: 1965-1974.

Simberloff, D., Stiling, P. (1996b) Risks of species introduced for biological control. *Biological Conservation* **78**: 185-192.

Soulé, M.E. (1990) The onslaught of alien species, and other challenges in the coming decades. *Conservation Biology* **4**: 233-239.

Syrett, P., Hill, R.L., Jessep, C.T. (1985) Conflict of interest in biological control of weeds in New Zealand. In: *Proceedings of the 6th International Symposium on Biological Control of Weeds* (Delfosse, E.S., Ed). Agriculture Canada, Vancouver, Canada. pp 391-377.

Thomas, W.P. (1989) *Epiphyas postvittana*, the lightbrown apple moth. In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 187-195.

Thomas, W.P., Hill, R.L. (1989) *Phyllonorycter messaniella*, oak leafminer (Lepidoptera: Gracillariidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 289-293.

Thomas, W.P., Walker, J.T.S. (1989) *Tetranychus urticae*, two-spotted mite (Acari: Tetranychidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 245-249.

Van Driesche, R.G. (1994) Biological control for the control of environmental pests. *Florida Entomologist* **77**: 20-33.

Van Driesche, R.G., Bellows, T.S. (1996) Biological Control. Chapman and Hall, New York, USA.

Van Driesche, R.G., Hoddle, M. (1997) Should arthropod parasitoids and predators be subject to host range testing when used as biological control agents ? *Agriculture and Human Values* **14**: 211-226.

Vitousek, P. M., D'Antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R. (1997) Introduced species: A significant component of human-caused global change. *New Zealand Entomologist* **21**: 1-16.

Walker, J.T.S. (1989) *Eriosoma lanigerum*, woolly apple aphid (Homoptera: Pemphigidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 197-199.

Walker, J.T.S., Wearing, C.H., Hayes, A.J. (1989) *Panonychus ulmi*, European red mite (Acari: Tetranychidae). In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 217-221.

Waterhouse, D.F., Norris, K.R. (1987) *Biological Control: Pacific Prospects*. Inkata, Melbourne, Australia.

Wilson, E.O. (1985) The biological diversity crisis: a challenge to science. *Issues in Science and Technology* **2**: 20-29.

Wise, K.A.J. (1953) Host plants of *Lithocolletis messaniella* (Lepidoptera: Gracillariidae) in New Zealand. *New Zealand Journal of Science and Technology* **35**: 172-174.

Wise, K.A.J. (1958) Notes on insect pests 1957-58. *New Zealand Entomologist* **1**: 27-30.

Zondag, R. (1975) Controlling Sirex with a nematode. *Proceedings of the 28th New Zealand Weed and Pest Control Conference*. pp 196-199.

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A record of the releases and recoveries of the Australian parasitoids *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) introduced into New Zealand for leafroller control.

ABSTRACT

The geographical ranges of the leafroller parasitoids *Xanthopimpla rhopaloceros* Krieger and *Trigonospila brevifacies* (Hardy) within New Zealand have not previously been determined. Records of establishment and dispersal from 1967-1996 are presented for both parasitoid species. *T. brevifacies* is present in the North and South Islands to 41°20'S and *X. rhopaloceros* is present in the North and South Islands to 41°48'S. Both parasitoids have been collected from islands off the coast of the North Island.

INTRODUCTION

The native Australian parasitoids *Xanthopimpla rhopaloceros* Krieger and *Trigonospila brevifacies* (Hardy) were introduced into New Zealand from Australia in 1967 to control the lightbrown apple moth, *Epiphyas postvittana* (Walker) (Tortricidae) (Thomas 1989). *T. brevifacies* was released at four North Island locations (Kerikeri, Hamilton, Tauranga and Havelock North) and two South Island locations (Nelson and Christchurch) in a series of releases from 1967-1987 (Thomas 1989; J. R. Clearwater, pers.comm., 1996). *X. rhopaloceros* was released at Kerikeri, Hamilton, Kaiangaroa, Rotorua, Nelson and Christchurch from 1967-1973 (Thomas 1989).

Concerns have since been raised because both species also attack non-target native Lepidoptera (Green 1984; Roberts 1986; Berry 1990). Early (1995) has also recorded the presence of the parasitoids on the Aldermen Islands, indicating that *X. rhopaloceros* and *T. brevifacies* are able to disperse across 20 km of continuous water and colonise conservation areas.

Determining the present geographical range of *T. brevifacies* and *X. rhopaloceros* is the first objective in a programme designed to determine the impact these biological control agents are having on non-target native lepidopterans. This paper documents the releases,

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redistribution and dispersal of *X. rhopaloceros* and *T. brevifacies* in New Zealand, using 29 years of collection records.

METHODS

Archival data

A request was made in the New Zealand Entomological Society newsletter for collection records of *X. rhopaloceros* and *T. brevifacies*. Written requests were also sent to curators of insect collections at research institutions, museums and universities. Records in the text and Appendix 1 are referred to by entomological region as defined by Crosby *et al.* (1976).

Field sampling

Field surveys were conducted in March/April 1996 at seven North Island sites and two South Island locations. Additional surveys were made at six of the North Island sites in October 1996, January 1997 and March 1997 to determine whether *X. rhopaloceros* and *T. brevifacies* were present in areas for which no archival data existed and to obtain additional data on the presence of the parasitoids in native habitats. Two 50 m transects were searched at each site and one caterpillar/pupa was taken approximately every two metres, giving a total of 40 individuals per site. Vegetation at each point along the transect was searched from ground level to 2 m for larvae or pupae. Samples were reared in the laboratory on general purpose diet (Singh, 1983) at 20°C, LD 16:8 and the resulting parasitoids and moths were then identified to species. The collection sites were: Rotoehu Forest (Bay of Plenty), native vegetation surrounded by *Pinus radiata* Don; Pongakawa Valley (BP), native forest remnant; Bushy Park, Kai Iwi (WI) native forest remnant in farmland; Totara Reserve, Pohangina Valley (WI), native forest remnant in farmland; a commercial orchard, Palmerston North; Tane, north-east of Eketahuna, Wairarapa native forest remnant in farmland ; Mt Bruce bush remnant (WI); Appleby Research Orchard, (NN); and Eve's Bush Reserve, (NN), adjacent to farmland and fruit crops. These field collections provided 1,080 caterpillars and 87 pupae, from the seven North Island and two Nelson, South Island sites.

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RESULTS AND DISCUSSION

Collection data were obtained from 12 institutions and six private collections. The present known distribution of the two parasitoids is shown in figure 1, and a full list of recoveries is given in Appendix 1.

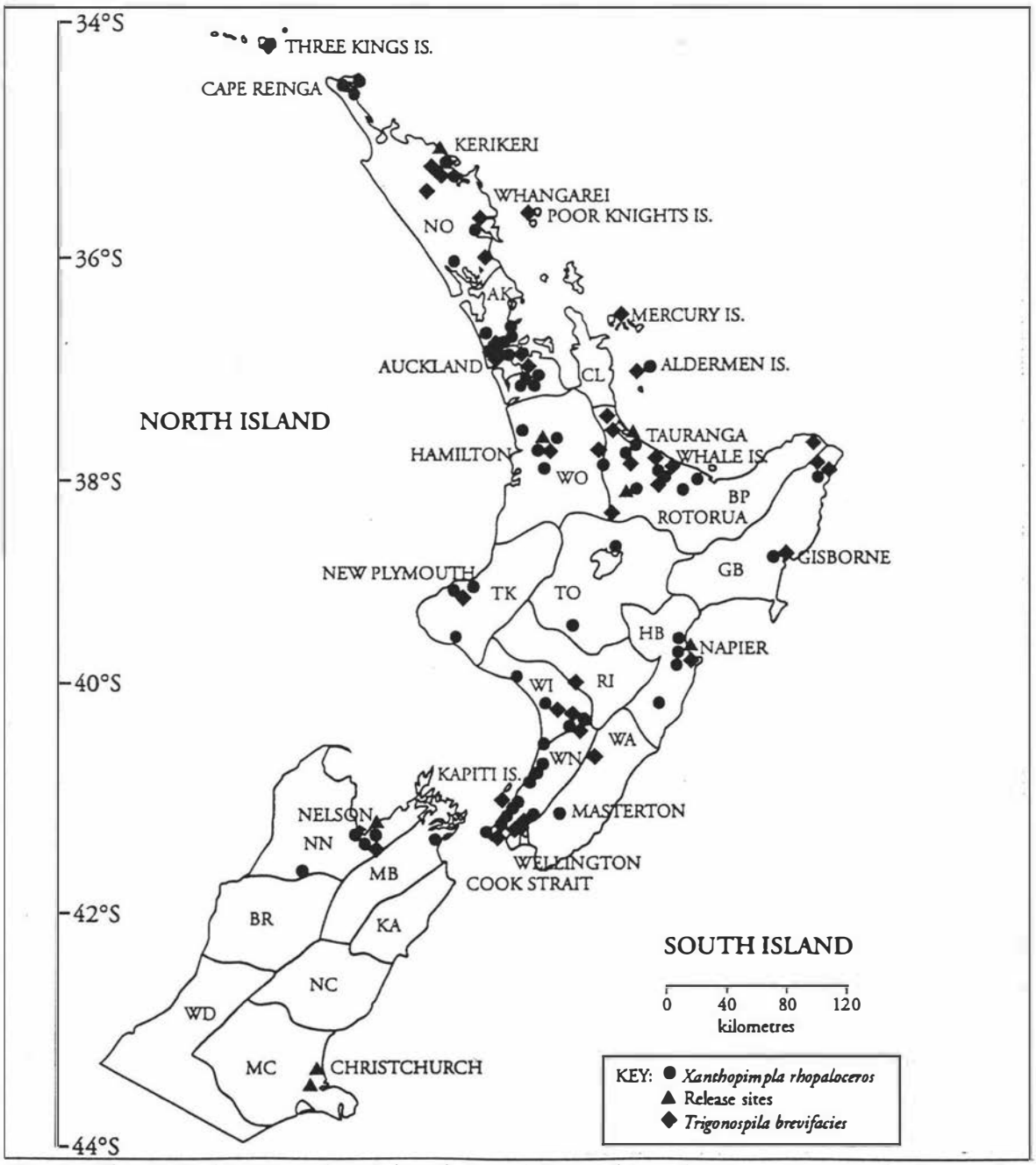

Figure 1. New Zealand locations where *T. brevifacies* and *X. rhopaloceros* have been released and subsequently collected between 1969 and 1996. Entomological Regions are shown for the North Island as: AK, Auckland; BP, Bay of Plenty; CL, Coromandel; GB, Gisborne; HB, Hawke's Bay; ND, Northland; RI, Rangitikei; TK, Taranaki; TO, Taupo; WA, Wairarapa; WI, Wanganui; WN, Wellington; WO, Waikato. South Island entomological regions are denoted as: BR, Buller; KA, Kaikoura; MB, Marlborough; MC, Mid-Canterbury; NC, North Canterbury; WD, Westland.

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Releases and redistribution

Propagules of approximately 200 *X. rhopaloceros* and *T. brevifacies* individuals per site were initially released in New Zealand (W.P. Thomas, pers.comm., 1996) from 1967-1973. Subsequent supplementary redistributions were made in both the North and South Islands until 1987. All available release and redistribution data for *X. rhopaloceros* and *T. brevifacies* are presented in Table 1.

Records of recoveries

T. brevifacies

The first record of *T. brevifacies* establishment came from Northland at Kerikeri in 1972 and was reported by R. A. Cumber (Thomas, 1989). In 1974-75, *T. brevifacies* was recorded in Northland parasitising *Ctenopseustis obliquana* (Walker) (Tortricidae) on kiwifruit and citrus crops and *Planotortrix notophaea* Turner (Tortricidae) in kiwifruit. However, no *T. brevifacies* were collected from any other regions during the 1974-75 DSIR/MAF National Survey of Leafrollers in New Zealand fruit crops (Wearing, 1994). By the early 1980s, *T. brevifacies* was established in several areas of Auckland. The first records of the species south of Auckland were at Hamilton in 1985, the Bay of Plenty in 1987 and at Wellington in 1988. During the 1990s, specimens of *T. brevifacies* have also been collected from the Wanganui (1990), Gisborne (1991), Wairarapa (1996), Taranaki (1996) and Hawkes Bay (1995/1996) entomological regions.

Between 20-26 *T. brevifacies* individuals collected in Auckland were redistributed for releases at Nelson, Lincoln, and Christchurch by DSIR staff (J.R. Clearwater, pers.comm., 1996) between 1981 and 1987. There were no records of *T. brevifacies* having established at these South Island sites by 1997 (W.P. Thomas, pers. comm., 1996; J. Marris, pers. comm., 1996). However, in the summer of 1997/98 several *T. brevifacies* were collected at Nelson. Because there were no post-release records of *T. brevifacies* in the South Island it is assumed that it has recently colonised the South Island from the North Island, rather than remaining undetected for 29 years in the South Island.

A redistribution of 19 *T. brevifacies* individuals was made by DSIR, to Havelock North, Hawkes Bay in 1981/82 (J.R. Clearwater, pers.comm., 1996), but it was not subsequently recorded until 1995 and 1996 from leafroller larvae collected from apple orchards

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Table 1. Release programme for *Xanthopimpla rhopaloceros* and *Trigonospila brevifacies* in New Zealand 1967-1987.

Release date	Location	Propagule size	Source	First record of establishment	Source
X. rhopaloceros					
1967-73	Kerikeri	approx. 200	Thomas 1989	1973	WPT pers. comm. 1996
1967-73	Hamilton	approx. 200	Thomas 1989	1973	WPT pers. comm. 1996
1967	Rotorua	approx. 200	Thomas 1989	1975	MJN pers. comm. 1996
1972	Kaiangaroa Forest	unknown	MJN pers.comm.	1981	Mckenzie 1981
1969	Nelson	12	Thomas 1989	briefly in late 1960s, reappeared 1989.	WPT pers. comm. 1996
1967-73	Christchurch	approx. 200	Thomas 1989	failed to establish	Thomas 1989
1980	Havelock North	approx. 200	JTSW pers.comm.	1985	JTSW pers. comm. 1996
1987	Havelock North	unknown	JRC pers.comm.	already established	JTSW pers. comm. 1996
Release date	Location	Propagule size	Source	First record of establishment	Source
T. brevifacies					
1967-72	Kerikeri	approx. 200	Thomas 1989	1972	Thomas 1989
1967-72	Hamilton	approx. 200	Thomas 1989	1985	HortResearch (Ruakura) collection
1967-72	Tauranga	approx. 200	Thomas 1989	1990	PANZ archive
1967	Appleby, Nelson	39	JRC pers. comm. 1996	failed to establish	WPT pers. comm. 1996
1969	Appleby, Nelson	20	JRC pers. comm. 1996	failed to establish	WPT pers. comm. 1996
1967-73	Christchurch	approx. 200	Thomas 1989	failed to establish	WPT pers. comm. 1996
1981	Havelock North	4	JRC pers. comm. 1996	1995/96	JTSW pers. comm. 1996
1981	Christchurch	20	JRC pers. comm. 1996	failed to establish	JRC unpub. data
1980s (early)	Appleby, Nelson	25	JRC pers. comm. 1996	failed to establish	JRC unpub. data
1982	Christchurch	25	JRC pers. comm. 1996	failed to establish	JRC unpub. data
1982	Havelock North	15	JRC pers. comm. 1996	1995/96	JTSW pers. comm. 1996
1987	Lincoln	26	JRC pers. comm. 1996	failed to establish	JRC unpub. data

WPT = W. P. Thomas, JRC= J. R. Clearwater, JTSW = J. T. S. Walker, NZAC = New Zealand Arthropod Collection, MJN = M. J. Nuttall, PANZ = Plant Protection Centre - Lynfield.

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near Havelock North (P. Lo, pers. comm., 1996). A population of *T. brevifacies* may have existed at undetected levels in the Hawkes Bay for 13 years after the initial releases (J.T.S. Walker, pers.comm., 1996). However, *T. brevifacies* was not reared from leafrollers collected in the Hawkes Bay during the 1980s, hence it may have recolonised Havelock North from other areas after the initial population failed to establish (J.G.Charles, pers. comm., 1997).

Xanthopimpla rhopaloceros

Xanthopimpla rhopaloceros was found to have established at a Nelson releases site in 1969. The first North Island records of *X. rhopaloceros* came from Kerikeri and Hamilton in 1973 and were reported by R. A. Cumber (Thomas, 1989) and B.B. Given respectively (W.P. Thomas, personal communication, 1996). In May 1975 E.W. Valentine noted that *X. rhopaloceros* populations had established at Auckland, Pukekohe, Hamilton, Arapuni, in the west to Kawhia, in the east at Tauranga, and to the east and west of Mt Taranaki (M.J. Nuttall, pers. comm., 1996).

Published reports from 1975/76 indicate that *X. rhopaloceros* occurred in such large numbers in Auckland that the general public began making inquiries to MAF about the species (MAF 1975, 1976). As no releases of the wasp had been made in Auckland, it was assumed that the area was colonised by individuals from the Hamilton or Kerikeri populations. Anecdotal evidence indicates that *X. rhopaloceros* is no longer so frequently observed in Auckland at least (J.R. Clearwater, pers. comm., 1996) and Roberts (1986) speculated that the larval parasitoid *T. brevifacies* may have displaced the pupal parasitoid *X. rhopaloceros*.

An unknown number of *X. rhopaloceros* were liberated in 1972 into Kaiangaroa Forest, Bay of Plenty (M.J. Nuttall, pers. comm., 1996). Mckenzie (1981) reported that the wasp was well established throughout the nearby Kinleith Forest. *X. rhopaloceros* was recorded in Wanganui in 1976 and at the DSIR Ballantrae Research Farm in the Manawatu in 1978. The species was collected at Taranaki in 1978, Kapiti coast in the late 1970s and Wellington in 1982. J.T.S. Walker (pers.comm., 1996) noted, during a leafroller survey of the Wanganui, Manawatu, and Hawkes Bay in the mid-1980s, that *X. rhopaloceros* was abundant in these regions.

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A collection of approximately 200 *X. rhopaloceros* from Nelson was redistributed to DSIR Havelock North Research Orchard in March 1980 and by 1985 it was abundant in the Havelock North area (J.T.S. Walker, pers.comm., 1996).

Further releases of *X. rhopaloceros* were made in Christchurch in 1972, 1978-1980 and 1984-1987, but a population failed to establish (Thomas, 1989). However, a population did establish at Nelson in the South Island in 1969. No further records of *X. rhopaloceros* occurred in the Nelson/Marlborough regions until 1992.

Field and archival data

Twenty-eight specimens of *T. brevifacies* emerged from samples collected at the Rotoehu Forest, Pongakawa Valley, Pohangina Valley, Huarau Orchard and Tane sites. The fly was not reared from larvae collected at the Mt Bruce, Bushy Park, Appleby or Eve's Bush sites.

No *X. rhopaloceros* emerged from the 87 pupae that were collected from nine field sites but *X. rhopaloceros* was observed on ornamental plants 5 km from the Rotoehu Forest site. Pupae are difficult to sample in large numbers and the absence of the parasitoid could have been due to the small sample sizes.

Fewer archival records of *T. brevifacies* were obtained compared with those of *X. rhopaloceros*. However, records of presence were obtained for both species in most areas of the North Island. More *X. rhopaloceros* have been collected than *T. brevifacies*, possibly because they established in quite high numbers initially (MAF, 1975) or because the species is a very obvious, predominantly yellow wasp that attracts attention. No specific follow-up monitoring was carried out at sites where *X. rhopaloceros* and *T. brevifacies* were released, and records of establishment were in most cases gathered during the course of other research. However, a National Survey of Leafrollers in Fruit Crops was conducted by the Department of Scientific and Industrial Research and Ministry of Agriculture and Fisheries in the three growing seasons 1974-75 to 1976-77, and this included records of all parasitism and diseases of eggs, larvae and pupae in the first season (Wearing 1994). This comprehensive survey was based on hundreds of samples (each comprising 1-2 hours of searching) on 16 crops in 11 regions, and included samples from shelter trees and other host plants in the orchard environment. The samples contained 15 species of Tortricidae and the gelechiid *Stathmopoda*

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sp. The 1974-75 data on parasitism are included in Appendix 1 and were derived from 299 samples containing 7075 leafrollers from throughout New Zealand. This survey provided a reasonable measure of the distribution of the parasitoids in fruit growing areas at that time.

Colonisation of islands

Since many offshore islands in New Zealand function as conservation areas for native plants and animals, it is of concern that *T. brevifacies* and *X. rhopaloceros* have established on some of these islands. It is most likely that dispersal by the parasitoids to these offshore islands was assisted by wind (Early 1995). *T. brevifacies* has been recorded on the Three Kings Islands, 58 km north west of Cape Reinga, in 1983. *T. brevifacies* has also been noted on the Poor Knights (1980), and on the Mercury Islands (1984), approx. 20 km and between 6-24 km respectively from the mainland. Both *T. brevifacies* and *X. rhopaloceros* have been collected on the Aldermen Islands, 20 km from the Coromandel Peninsula (Early 1995). *X. rhopaloceros* has not been collected from Kapiti Island (J. McCartney, pers.comm., 1996), although *X. rhopaloceros* has occurred on the Kapiti coast, 6 km distant, since the early 1980s. *T. brevifacies* has been present in the Kapiti district since the late 1980s and was recently collected from Kapiti Island (Appendix 1). A recent week long invertebrate survey of Moutohora Island (also known as Whale Island) failed to find *T. brevifacies* or *X. rhopaloceros* (Patrick 1996), despite *T. brevifacie's* occurrence on the mainland between Te Puke and Whakatane. Other islands that should be investigated for the presence of the parasitoids are those in Cook Strait.

CONCLUSIONS

The northern-most record for *T. brevifacies* on the mainland is at Kerikeri and it has also colonised Great Island in the Three Kings group, 50 km north of the North Island. *X. rhopaloceros* occurs at the northern extreme of the North Island, but unlike *T. brevifacies* has not colonised the Three Kings Islands.

X. rhopaloceros and *T. brevifacies* have colonised locations along the east coast of the North Island in Northland, Auckland, Bay of Plenty, Gisborne and Hawkes Bay.

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On the west coast, *X. rhopaloceros* has been collected at Cape Reinga, Auckland and the Taranaki, Wanganui, Wellington and Nelson regions. *T. brevifacies* occurs along the west coast of the North Island in the Auckland, Taranaki and Wellington regions.

Records for the fly *T. brevifacies* show that it has established as far south as Nelson in the South Island. Recent records of *X. rhopaloceros* indicate that it is present as far south as Murchison, Nelson and Blenheim in the South Island (W.P. Thomas, personal communication, 1996). It has not been confirmed whether the pattern of distribution of *X. rhopaloceros* and *T. brevifacies* is continuous across the Cook Strait, including the Marlborough Sounds and islands.

Although under certain weather conditions Australian insects, including Ichneumonidae (Gauld 1984), have dispersed across the Tasman Sea to the west coast of New Zealand (Fox 1974), it is assumed that the present geographical range for *T. brevifacies* and *X. rhopaloceros* has occurred since the release of these species in the late 1960s. No specimens of *T. brevifacies* or *X. rhopaloceros* are known from New Zealand prior to their release.

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REFERENCES

Berry, J. A., 1990: Two parasitoid complexes: *Hierodoris atychioides* (Butler) (Lepidoptera: Oecophoridae) and *Icerya purchasi* (Maskell) (Homoptera: Margarodidae). *New Zealand Entomologist* 13: 60-62.

Crosby, T. K., Dugdale, J. S., Watt, J. C., 1976: Recording specimen localities in New Zealand: an arbitrary system of areas and codes defined. *New Zealand Journal of Zoology* 3: 69 plus map.

Early, J. W., 1995: Insects of the Aldermen Islands. *Tane* 35: 1-14.

Fox, K.J., 1974: Trans-oceanic dispersal of insects in New Zealand. *New Zealand Entomologist* 5: 240-243.

Gauld, I.D., 1984: The Australian Ophioninae (Insecta: Hymenoptera): a historical biogeography study. *Journal of Biogeography* 11: 269-288.

Green, O. R., 1984: New Zealand host and locality records for an introduced tortricid parasite, *Trigonospila brevifacies* (Diptera: Tachinidae). *New Zealand Entomologist* 8: 69-71.

M.A.F., 1975: *Monthly Circular, January 1975*. Auckland Plant Health and Diagnostic Station.

M.A.F., 1976: *Monthly Circular, March 1976*. Auckland Plant Health and Diagnostic Station.

Mckenzie, R. J. M., 1981: *Xanthopimpla rhopaloceros*. *Forest Biology Observer*, monthly report for March 1981, south-west Rotorua.

Patrick, B. H., 1996: Invertebrates of Moutohora. *Technical Report Series* No 24. Department of Conservation, Rotorua, New Zealand

Roberts, L. I. N., 1986: The practice of biological control - implications for conservation, science and community. *The Weta* **9,** 76-84.

Singh, P., 1983: A general purpose laboratory diet mixture for rearing insects. *Insect Science and its Application 4*: 357-362.

Thomas, W. P., 1989: *Epiphyas postvittana*, the lightbrown apple moth. Pp 187-195 In Cameron, P.J.; Hill, R.L.; Bain, J.; Thomas, W.P. (Eds): *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987*. CAB International, Wallingford, U.K.

Wearing, C.H., 1994: National Leafroller Survey: Species Distribution Charts for Crops and Regions. *HortResearch Internal Report No. IR 94-64*: 51 pp.

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APPENDIX 1 : Recoveries of *Trigonospila brevifacies* and *Xanthopimpla rhopaloceros*

Trigonospila brevifacies
(NBD = no biological data; - = month unknown)

Year	Location	Entomological Region	Collection details
1972 -	Kerikeri	Northland	ex tortricid larva, citrus orchard
1974 Nov	Kerikeri	Northland	ex tortricid larva, kiwifruit orchard
1974 Nov	Kerikeri	Northland	ex tortricid larva, kiwifruit orchard
1974 Nov	Kerikeri	Northland	ex tortricid larva, kiwifruit orchard
1975 Jan	Kerikeri	Northland	ex tortricid larva, grapefruit orchard
1977 Mar	Omahuta Sanctuary	Northland	NBD
1980 Nov	Remuera	Auckland	ex tortricid larva on *Hebe parviflora*
1980 Dec	Poor Knights I.	Northland	NBD
1980 Dec	Auckland	Auckland	ex tortricid larva
1980 Dec	Riverhead Forest	Auckland	exotic forest
1981 Jan	Huapai	Auckland	ex tortricid larva
1981 Mar	Titirangi	Auckland	NBD
1981 Mar	Auckland	Auckland	urban garden
1981 Jul	Whangarei	Northland	urban garden
1981 Aug	Mt Albert	Auckland	orchard
1981 Aug	Wattle Bay	Auckland	NBD
1981 Oct	Wattle Bay	Auckland	NBD
1981 Dec	Remuera	Auckland	dwelling
1982 Jan	Kumeu	Auckland	orchard
1982 Jan	Kumeu	Auckland	orchard
1982 Jan	Kumeu	Auckland	orchard
1982 Mar	Albany	Auckland	orchard
1982 May	Henderson	Auckland	ex tortricid larva, garden on *Hebe* sp.
1982 May	Henderson	Auckland	ex tortricid larva, garden on *Hebe* sp.
1982 Jul	Kerikeri	Northland	orchard
1982 Sep	Howick	Auckland	garden
1982 Oct	Manurewa	Auckland	dwelling
1982 Dec	Whangarei	Northland	ex tortricid larva
1982 Dec	Pukekohe	Auckland	dwelling
1983 Feb	Auckland	Auckland	NBD
1983 Feb	St Marys Bay	Auckland	NBD
1983 Jul	Titirangi	Auckland	ex Psychidae case
1983 Aug	Mt Albert	Auckland	on leaf, *Linum* sp.
1983 Dec	Great Island,Three Kings Is	Northland	native habitat
1984 Feb	Western Springs	Auckland	sweep-netted
1984 Feb	Middle Mercury Is	Coromandel	native habitat
1984 Mar	Massey	Auckland	ex tortricid larva, on *Leptospermum* sp.
1984 Aug	Whangarei	Northland	urban garden
1984 Oct	Atuarui	Auckland	ex tortricid larva
1985 Jan	Mangawhai Heads	Northland	ex tortricid larva
1985 Mar	-	Waikato	ex tortricid larva
1985 -	Hamilton	Waikato	boysenberry crop
1985 Nov	Lynfield	Auckland	NBD
1986 Dec	Tuakau	Auckland	dwelling
1987 Jun	Mamaku Plateau	Bay of Plenty	ex tortricid larva

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Trigonospila brevifacies (continued)

Year	Location	Entomological Region	Collection details
1987 Oct	Weymouth	Auckland	ex tineid larva
1988 Jan	Auckland	Auckland	urban garden
1988 Oct	Lower Hutt	Wellington	garden
1988 Dec	Wellington	Wellington	NBD
1980's late	Levin	Wellington	garden
1989 Feb	Tahuna Torea Nat.Res	Auckland	on *Convolvulus* sp.
1989 Mar	Whangarei	Northland	NBD
1989 Sep	Oratia	Auckland	ex Lepidoptera pupa on *Rubus* sp.
1990 Mar	Auckland	Auckland	garden
1990 May	Wellington	Wellington	NBD
1990 Jun	Tauranga	Bay of Plenty	dwelling
1990 Sep	Massey University	Wanganui	native vegetation
1991 Sep	Awapuni	Waikato	mandarin tree
1991 Dec	Te Rereauira Swamp	Bay of Plenty	NBD
1991 Dec	Waenga Bush	Bay of Plenty	NBD
1991 Dec	Taikawakawa	Gisborne	NBD
1991 Dec	Grey's Bush	Gisborne	NBD
1992 May	Palmerston North	Wanganui	garden
1993 Feb	Upper Hutt	Wellington	NBD
1993 Mar	Palmerston North	Wanganui	garden
1993 Mar	Massey University	Wanganui	on flowers
1993 Jun	Palmerston North	Wanganui	garden
1993 Nov	Te Kanapa Stream	Gisborne	ex tortricid larva
1994 May	Palmerston North	Wanganui	garden
1994 Dec	Aldermen Islands	Bay of Plenty	native habitat
1995 Mar	Kaimai Range	Bay of Plenty	ex tortricid larva
1995 Mar	Havelock North	Hawkes Bay	apple orchard, ex tortricid larva
1995 Apr	Tauranga	Bay of Plenty	fruit fly trap
1995 Jun	Havelock North	Hawkes Bay	apple orchard, ex tortricid larva
1995 Aug	Palmerston North	Wanganui	garden
1996 Feb	Waipukurau	Hawkes Bay	on flower
1996 Mar	Tane	Wairarapa	on *Forsythia* sp. in garden
1996 Mar	Palmerston North	Wanganui	pear orchard ex tortricid larva
1996 Mar	Palmerston North	Wanganui	on flower, *Hebe* sp.
1996 Mar	Katikati	Bay of Plenty	garden
1996 Mar	New Plymouth	Taranaki	garden
1996 Apr	Havelock North	Hawkes Bay	apple orchard, ex tortricid larva
1996 Apr	Palmerston North	Wanganui	on leaves *Populus* sp., of orchard shelter
1996 Apr	Tane	Wairarapa	ex tortricid larva from native bush
1996 Apr	Pongakawa	Bay of Plenty	poplar shelter in kiwifruit orchard
1996 Apr	Pongakawa valley	Bay of Plenty	on flower, *Dahlia* sp.
1996 Apr	Rotoehu Forest	Bay of Plenty	ex tortricid larva from native forest
1996 Apr	Pongakawa valley	Bay of Plenty	ex tortricid larva from native forest
1996 Apr	Patumahoe	Waikato	sweep net over grass
1996 Apr	Totara Res., Palmerston North	Wanganui	sweep net in native vegetation
1996 Apr	Halcombe	Wanganui	on flower, *Rosa* sp.
1996 May	Palmerston North	Wanganui	dwelling
1996 May	Palmerston North	Wanganui	dwelling

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Trigonospila brevifacies (continued)

Year	Location	Entomological Region	Collection details
1996 May	Palmerston North	Wanganui	on *Agapanthus* sp.
1996 Aug	Tane	Wairarapa	in rural garden, on *Lonicera* sp.
1996 Oct	Tane	Wairarapa	in rural garden, on *Amaryllis belladonna*
1998 Jan	Nelson	Nelson	collected from urban garden
1998 Jan	Kapiti I.	Wellington	male basking on *Melicytus ramiflorus*
1998 Mar	Nelson	Nelson	in house

Xanthopimpla rhopaloceros

Year	Location	Entomological Region	Collection details
1969 Apr	Nelson	Nelson	NBD
1969 Jul	Nelson	Nelson	ex tortricid from apple research orchard
1973 -	Kerikeri	Northland	ex tortricid, citrus orchard
1973 -	Hamilton	Waikato	NBD
1974 Feb	Hamilton	Waikato	urban garden
1975 Jan	Hamilton	Waikato	garden in large numbers on ornamentals
1975 Feb	Tauranga	Bay of Plenty	on ornamental plants
1975 Mar	Maramarua Forest	Auckland	exotic forest
1975 May	New Plymouth	Taranaki	on wing over hedge
1975 May	Rotorua	Bay of Plenty	urban garden, resting on *Ceanothus* sp.
1975 May	Rotorua	Bay of Plenty	garden
1975 Jun	Waitangi Forest	Northland	native vegetation
1975 Jun	Waitangi Forest	Northland	exotic vegetation
1975 Dec	Rotorua	Bay of Plenty	dwelling
1976 Mar	Rotorua	Bay of Plenty	NBD
1976 Mar	Rotorua	Bay of Plenty	Research Institute grounds
1976 Mar	Rotorua	Bay of Plenty	NBD
1975 Apr	Auckland	Auckland	urban garden
1976 Apr	Wanganui	Wanganui	NBD
1977 Feb	Manurewa	Auckland	NBD
1977 May	Rotorua	Bay of Plenty	in Forest Research Institute grounds
1977 May	Takapuna	Auckland	netted in *Leptospermum* sp. shrubland
1977 May	Takapuna	Auckland	netted on *Acmena* sp. hedge
1978 Feb	Milford	Auckland	NBD
1978 Mar	Ballantrae	Wairarapa	light trap in pastoral landscape
1978 Mar	Rotorua	Bay of Plenty	NBD
1978 May	Hawera	Taranaki	lemon tree in urban garden
1978 Jun	Shannon	Wellington	ex tortricid pupa
1978 Dec	Glenview, Hamilton	Waikato	urban garden
1979 Jan	New Plymouth	Taranaki	NBD
1979 Jan	Glenview, Hamilton	Waikato	urban garden
1979 Jan	Takapuna	Auckland	NBD
1979 Jan	Glenview, Hamilton	Waikato	urban garden
1979 Feb	Milford	Auckland	NBD
1979 Mar	New Plymouth	Taranaki	NBD
1979 Mar	Palmerston North	Wanganui	urban garden
1979 Apr	Otaki	Wellington	NBD
1979 Apr	Wanganui	Wanganui	urban garden

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Xanthopimpla rhopaloceros (continued)

Year	Location	Entomological Region	Collection details
1979 Apr	Foxton Beach	Wanganui	NBD
1979 Apr	Whakatane	Bay of Plenty	dwelling
1979 May	Palmerston North	Wanganui	NBD
1979 Oct	Rotorua	Bay of Plenty	NBD
1979 -	Levin	Wellington	garden
1980 -	Birkenhead	Auckland	NBD
1980 Jan	South Auckland	Auckland	NBD
1980 Jan	Auckland	Auckland	urban garden
1980 Feb	Tauranga	Bay of Plenty	grape vine
1980 Apr	Waitara	Taranaki	NBD
1980 Jun	Havelock North	Hawkes Bay	NBD
1980 Oct	Titirangi	Auckland	malaise trapped
1980 Dec	Levin	Wellington	ex Lepidoptera larva
1981 Feb	Rotorua	Bay of Plenty	NBD
1981 Mar	Gisborne	Gisborne	urban garden
1981 Mar	Upper Hutt	Wellington	NBD
1981 Apr	Otaki	Wellington	garden
1981 Apr	Porirua	Wellington	NBD
1981 May	Waikanae	Wellington	NBD
1981 Oct	Tauranga	Bay of Plenty	NBD
1982 Apr	Paekakariki	Wellington	NBD
1982 Feb	Kawerau	Bay of Plenty	urban garden
1982 Mar	Albany	Auckland	orchard
1982 Apr	Hataitai	Wellington	NBD
1982 Apr	Te Kaaka	Gisborne	fruit tree in farmland
1982 May	Upper Hutt	Wellington	NBD
1982 May	Te Awamutu	Waikato	pastoral landscape
1982 Jul	Kerikeri	Northland	orchard
1983 Feb	Kawakawa	Northland	NBD
1983 Apr	Wanganui	Wanganui	NBD
1983 Apr	Taupo	Taupo	ex tortricid larva
1983 -	Nelson	Nelson	Appleby Research Orchard
1983 Aug	Hamilton	Waikato	urban garden
1985 -	Hamilton	Waikato	boysenberry crop
1985 Jan	Shannon	Wellington	dwelling
1985 Feb	Feilding	Wanganui	urban garden
1985 Mar	Wellington	Wellington	NBD
1985 May	Waikanae	Wellington	NBD
1985 May	Wellington	Wellington	NBD
1985 May	Lower Hutt	Wellington	NBD
1985 Jun	Wellington	Wellington	NBD
1987 Jan	St Johns	Auckland	NBD
1987 Jan	Tawa	Wellington	NBD
1987 Feb	Onehunga	Auckland	NBD
1987 Oct	Weymouth	Auckland	ex Lepidopteran larva
1988 Mar	Mt Albert	Auckland	urban garden, on *Leptospermum* sp.
1988 Apr	Kumeu	Auckland	NBD
1988 May	Bulls	Wanganui	plant nursery

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Xanthopimpla rhopaloceros (continued)

Year	Location	Entomological Region	Collection details
1989 Jan	Blenheim	Marlborough	urban
1989 Feb	Naike	Waikato	NBD
1989 Feb	Nelson	Nelson	NBD
1989 Mar	Nelson	Nelson	ex tortricid pupa, on *Ulmus* sp.
1989 May	Auckland	Auckland	urban garden on *Eucalyptus* sp.
1989 Aug	Mt Maunganui	Bay of Plenty	native vegetation
1989 Nov	Haumoana	Hawkes Bay	ex Lepidoptera larva
1990 Mar	Whenuapai	Auckland	NBD
1990 Feb/Mar	Appleby Research Orchard	Nelson	in tortricid pheromone trap
1990 Mar	St Marys Bay	Auckland	NBD
1990 Mar	Massey University	Wanganui	on leaves, *Eucalyptus* sp.
1990 Nov	Rotoehu Forest	Bay of Plenty	exotic forest
1991 Jan	Castor Bay	Auckland	NBD
1991 Mar	Pohangina Valley	Wanganui	native forest
1991 Mar	Bethells Beach	Auckland	NBD
1991 Apr	Massey University	Wanganui	sweep netted over grass
1991 Jun	Napier	Hawkes Bay	NBD
1991 Jun	Blenheim	Marlborough	NBD
1991 Jul	Torbay	Auckland	NBD
1991 Aug	Hamilton	Waikato	pheromone lure trap
1992 Mar	Richmond	Nelson	public gardens
1992 Mar	Wakefield	Nelson	NBD
1992 Apr	Blenheim	Marlborough	public gardens
1992 May	Woodhill Forest	Auckland	exotic forest
1993 Apr	Bulls	Wanganui	plant nursery ex tortricid
1993 May	Masterton	Wairarapa	dwelling
1993 May	Te Awamutu	Waikato	sweep netted
1993 May	Taupo	Taupo	urban garden
1993 Jul	Okahu	Northland	in car
1994 Apr	Murchison	Nelson	NBD
1994 Dec	Aldermen Is	Bay of Plenty	native habitat
1995 Jan	Nelson	Nelson	apple orchard
1995 Mar	Totara Reserve	Wanganui	native vegetation
1995 Mar	Momotu Stream,Kaimai Ra.	Bay of Plenty	ex Lepidoptera larva, native habitat
1995 Dec	Cape Reinga	Northland	NBD
1995 Dec	Te Paki	Northland	NBD
1996 Apr	Pongakawa Valley	Bay of Plenty	in rural garden, on *Dahlia* sp.
1996 Feb	Te Paki	Northland	on the wing
1996 Feb	Stoke	Nelson	NBD
1996 Feb	Aokautere	Wanganui	exotic plantation
1996 Mar	Palmerston North	Wanganui	on *Callistemon* sp.
1996 Apr	Paturnahoe	Waikato	on *Hibiscus* sp.
1996 Apr	Ohakune	Taupo	on *Hebe stricta*
1996 Apr/May	Richmond	Nelson	ex Tortricidae pupa, on boysenberries

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A retrospective analysis of the establishment and dispersal of the introduced Australian parasitoids *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) within New Zealand.

ABSTRACT

Two Australian parasitoids, *Xanthopimpla rhopaloceros* Krieger and *Trigonospila brevifacies* (Hardy), were introduced to New Zealand to control the lightbrown apple moth (*Epiphyas postvittana* (Walker)). Dispersal by the parasitoids has since occurred naturally and with the aid of releases in fruit growing areas. The present geographical range of the parasitoids includes all the North Island and some offshore islands to latitude 41° 20'S. *X. rhopaloceros* is also present to latitude 41°48'S in the South Island and *T. brevifacies* has recently colonised the northern South Island at 41°18'S. Comparisons of these distributions with those in Australia indicate that climatic conditions may have played a major role in the areas of establishment of both species in New Zealand. Mean winter temperature may be a limiting factor in the dispersal of *T. brevifacies* and *X. rhopaloceros* in New Zealand. Other factors which have probably aided the successful dispersal of the parasitoids include the wide distribution of host Tortricidae and the occurrence of tortricid host plants. Areas of New Zealand which appear suitable for further colonisation by *T. brevifacies* include northern areas of the South Island, and both parasitoids could disperse further south into suitable climate areas of the east and west coasts of central South Island. Rate of dispersal for *X. rhopaloceros* was estimated at 13-24 km per year and for *T. brevifacies* at 8-15 km per year.

INTRODUCTION

The Australian parasitoids *Xanthopimpla rhopaloceros* (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Diptera: Tachinidae) were intentionally released in New Zealand as part of a classical biological control programme against the lightbrown apple moth *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), an orchard pest of Australian origin, between 1967 and 1973. *Xanthopimpla rhopaloceros* is a parasitoid of lepidopteran pupae

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and *T. brevifacies* is a parasitoid of late-instar lepidopteran larvae. These parasitoids have since established widely in New Zealand (Thomas, 1989; Munro, 1998).

Founders of the New Zealand populations of both parasitoids were collected from eastern Australia and Tasmania during the summers of 1967 and 1969 (Thomas, 1989). Most of the parasitoids came from the Mornington Peninsula, an apple-growing area in Victoria. They were also collected from research orchards in the Huon Valley, Tasmania, and from Gininderra, near Canberra, in the Australian Capital Territory (W.P. Thomas, personal communication, 1996).

The distribution of the Indo-Australian genus *Xanthopimpla* is largely tropical (Townes & Chiu, 1970) with a wide geographical range, including northern tropical Australia (Naumann, 1991), Sri Lanka (R. Kfir, pers.comm.), West Java and Sabah in Eastern Malaysia (Sankaran & Syed, 1972), the Indian regions of Kerala (Pillai & Nair, 1990), Punjab (Sran & Sandhu, 1979), Karnataka (Singh, 1992), Gujarat (Kapadia, 1987), Tamil Nadu (Pillai & Nair, 1989), and the Chinese provinces of Guangxui and Hunan (Wang & Liu, 1994). *Xanthopimpla* species have also been recorded in the Indo-Australian areas of the Philippines, Papua New Guinea and Borneo (Townes & Chiu, 1970). The distributions of *Xanthopimpla* species expanded by releases as biological control agents in Mauritius (Williams, 1983), South Africa (Kfir, 1991; 1994), and the USA (Hailemichael *et al*. 1994). *X. rhopaloceros* has been collected from coastal northern Australia, Western Australia, New South Wales, Victoria, South Australia and Tasmania (Townes & Chiu, 1970).

Trigonospila is a non-endemic genus found in Australia, Eurasia and tropical Africa (Crosskey, 1973). Few data have been published on *T. brevifacies* in New Zealand, apart from some host range and location data (Green, 1984; Thomas, 1989; Berry, 1990). In Australia, *T. brevifacies* has been recorded in Victoria, associated with tortricids feeding on capeweed (*Arctotheca calendula* Levyns) (Cordingley & Danthanarayana, 1976). Records from the Australian National Insect Collection (P. Cranston, personal communication, 1996) verify that *T. brevifacies* has been collected in the states of New South Wales, The Australian Capital Territory, Victoria, South Australia, south-west Western Australia and in Tasmania. *T. brevifacies* has not specifically been used in any integrated pest management initiative against *E. postvittana* in Australia (W. Danthanarayana, pers. comm., 1996), although a

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Trigonospila species was recorded as part of a parasitoid complex associated with *E. postvittana* during a long term study in Victoria (Danthanarayana & Farrugia, 1977).

Munro (1998) reported the details of the releases and recoveries of *X. rhopaloceros* and *T. brevifacies* in New Zealand. The aims of this paper are to document the dispersal and present geographical range of the parasitoids and to analyse retrospectively the factors contributing to the successful establishment of *X. rhopaloceros* and *T. brevifacies* within New Zealand. Habitat types and climate regions from which these species have been reported are also presented.

METHODS AND MATERIALS

Insect data

Records were obtained from specimens held in 18 New Zealand insect collections. These archival data (Munro, 1998), were combined with field data (see Munro, 1998 for methods) to construct a map of the present geographical range of the parasitoids.

Australian distribution data for *X. rhopaloceros* and *T. brevifacies* were obtained from the Division of Entomology C.S.I.R.O, Canberra; Museum of Victoria, Melbourne and the Department of Primary Industries, Tasmania.

Rates of dispersal of the parasitoids in New Zealand were estimated by comparing dates of releases with dates of recoveries at different locations.

Climate data

Climate data for locations where *X. rhopaloceros* and *T. brevifacies* were collected in Australia and New Zealand were compiled using Garnier (1958), Dwyer (1958) and Gentilli (1971).

RESULTS

Rates of dispersal.

Following releases of approximately 200 individuals at Hamilton and Kerikeri in the North Island between 1967 and 1972 (W.P. Thomas, personal communication, 1996), *X. rhopaloceros* was first recorded in Auckland 8 years later. Auckland is 195 km south of Kerikeri and 105 km north of Hamilton, giving *X. rhopaloceros* a dispersal rate of between 13 and 24 km/year. E. W. Valentine noted that *X. rhopaloceros* had dispersed 175 km, to the

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west of the North Island from its Hamilton release site, by May 1975 (Munro, 1998). This gives the wasp a dispersal rate of approximately 22 km/year in this instance. *X. rhopaloceros* was released at Rotorua in the central North Island in the late 1960s. By 1981, it had crossed the eastern cape, 250 km away, thus dispersing at a rate of 18 km/year.

Data about the progressive establishment of *T. brevifacies* in the North Island is provided by records from uninhabited offshore islands where natural dispersal is the only feasible mode by which the fly could colonise these areas. It was confirmed that *T. brevifacies* had established at its release site at Kerikeri in the northern North Island by 1972. It was recorded 58 km offshore on Great King Island in 1983, an estimated dispersal rate of 13 km/year. The Poor Knights Islands were probably colonised from the same release site, a distance of 75 km. The first record of *T. brevifacies* on the Poor Knights was in 1980 giving an estimated dispersal rate of 19 km/year. The Mercury Islands, another group of islands east of the central North Island mainland, was colonised by the fly in 1984. Using the distances of the three closest release sites to the Mercury Islands, Kerikeri, Hamilton and Tauranga, it is estimated that *T. brevifacies* dispersed at a rate of 8-12 km/year to reach this island group. The fly was first recorded on the Aldermen Islands, situated 20 km from the mainland, in 1994 with an estimated dispersal rate of 4 km/year from the nearest release site at Tauranga. *Trigonospila brevifacies* was first recorded in Auckland in 1980, an estimated dispersal rate of 8 or 15 km per year from the release sites at Kerikeri and Hamilton respectively.

Anecdotal evidence that *X. rhopaloceros* arrived earlier than *T. brevifacies* at non-release sites throughout the North Island is confirmed by the collection records (Munro, 1998). *Xanthopimpla rhopaloceros* dispersed at an estimated average rate of 19.2 km/year, while *T. brevifacies* dispersed at an average of 11.2 km/year.

Present geographical range in New Zealand

The present geographical ranges of *T. brevifacies* and *X. rhopaloceros* are presented in Figure 1. Field survey results and archival data (Munro, 1998) provided positive records for 99 sites with *T. brevifacies* and 130 sites with *X. rhopaloceros* in the North Island, northern South Island and some offshore islands, (named in Fig. 1).

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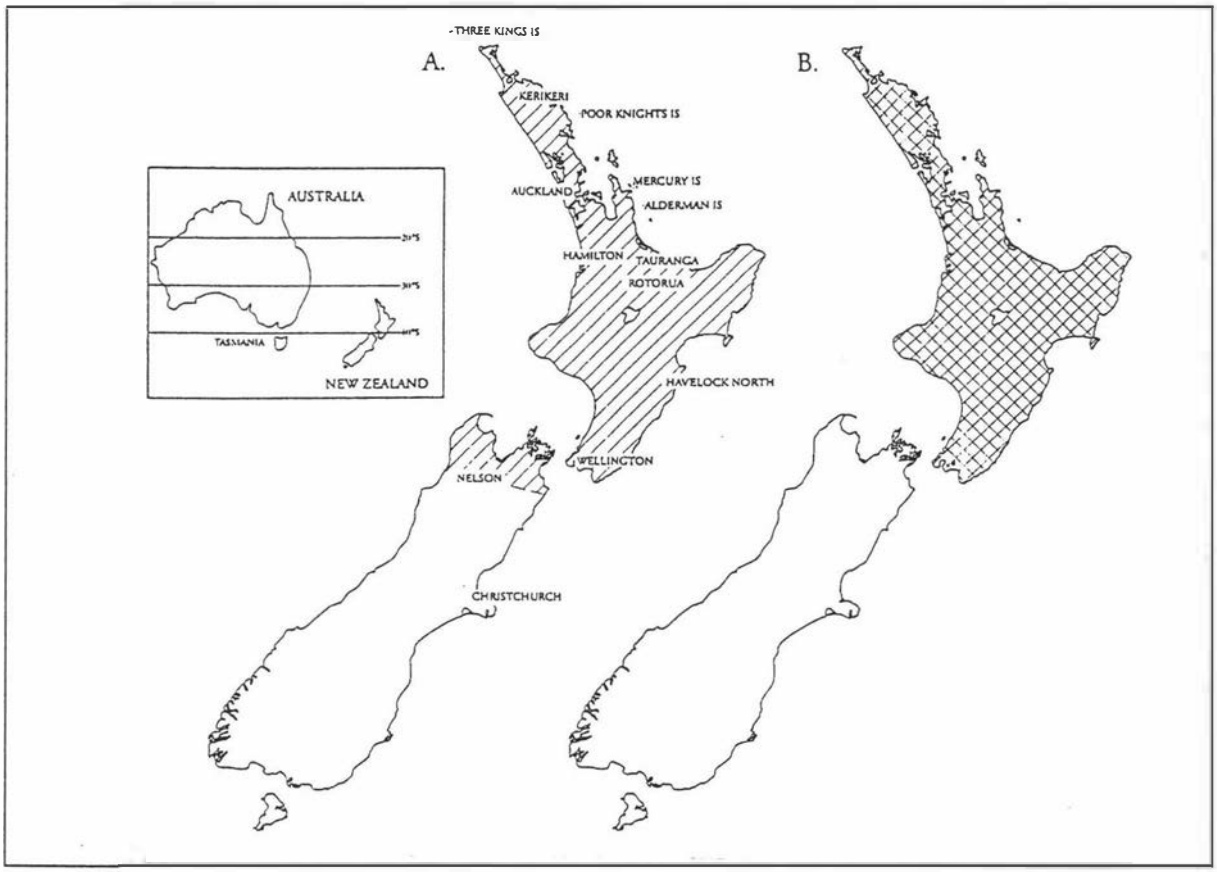

Figure 1. Geographical range of (*A*) *X. rhopaloceros* and (*B*) *T. brevifacies* in New Zealand. The inset shows the latitudinal relationship of New Zealand to Australia.

Climate comparisons between sites of origin in Australia and sites of release and establishment in New Zealand.

Figure 2 shows the Australian locations where individuals of *X. rhopaloceros* and *T. brevifacies* were collected for introduction into New Zealand (W.P. Thomas, personal communication, 1996). The collection sites were the Mornington Peninsula (latitude 38 °10' S), an apple growing area south of Melbourne, Victoria;. Gininderra, in the Australian Capital Territory near Canberra (latitude 35°17'S); and the Huon Valley (latitude 43° 0'S), south of Hobart, Tasmania. Figure 2 also shows distribution records for *X. rhopaloceros* and *T. brevifacies* in Australia.

Areas of New Zealand that are climatically similar, in terms of mean annual rainfall, mean annual temperature, mean summer temperature and mean winter temperature to Melbourne, Canberra and south eastern Tasmania are identified in Figure 3.

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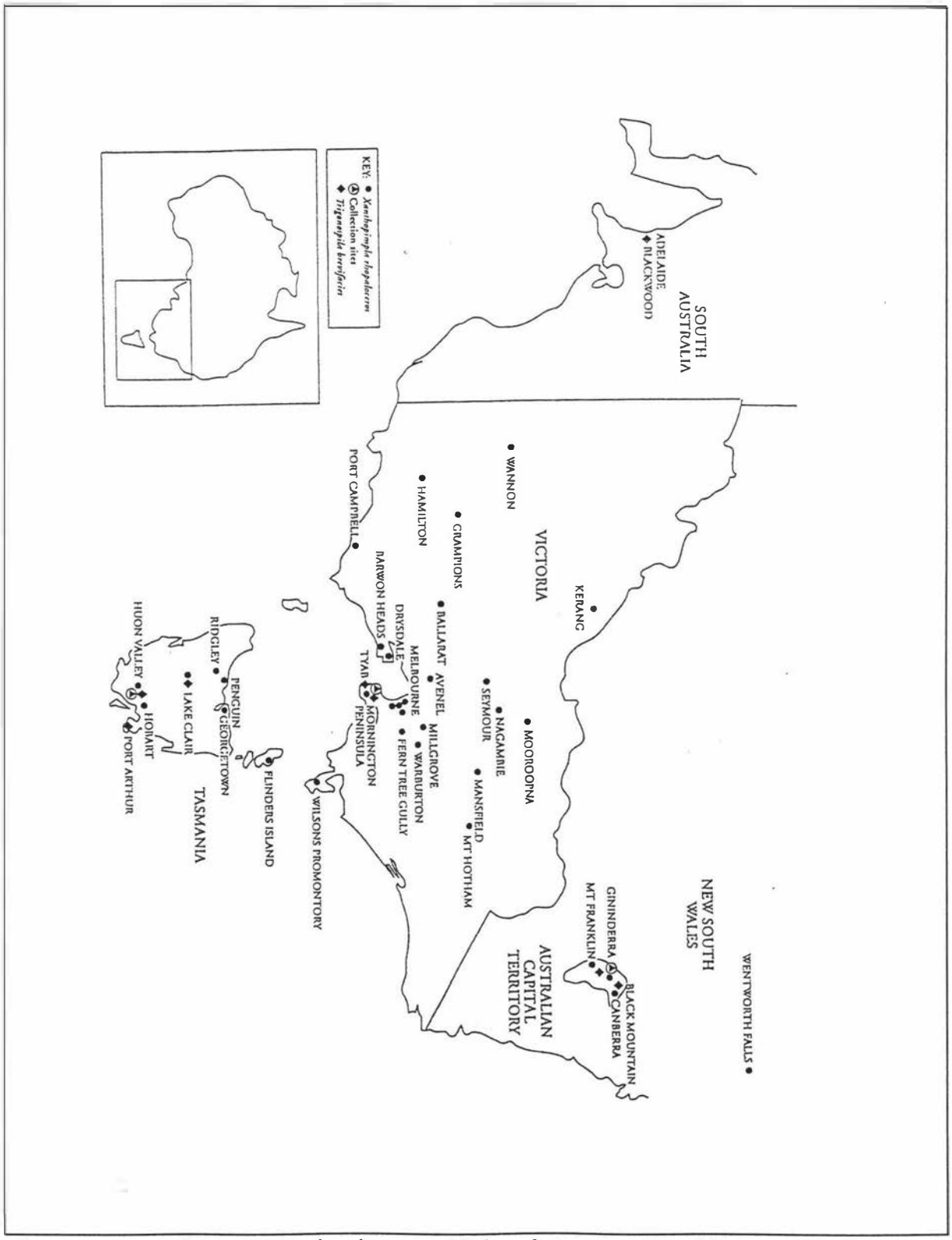

Figure 2. Locations from which *X. rhopaloceros* and *T. brevifacies* were collected for introduction into New Zealand and locations where records indicate that *X. rhopaloceros* and *T. brevifacies* occur in Australia.

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Most areas of the North Island have mean annual temperatures within the range of 12°C-14°C, which is similar to the mean annual temperature range for Canberra, Melbourne and Hobart (Fig. 3A). Both parasitoids have colonised the North Island (Fig. 1). The month with coolest mean temperatures in New Zealand and all three Australian collection sites is July (Gentilli, 1971). The mean July temperature for Melbourne is 9.6°C, which falls into the July temperature range for the east and west of the central North Island of New Zealand. Mean July temperatures for Canberra (6°C) and Hobart (6.7°C) fall into the 6-7°C mid-winter temperature range found in the central South Island (Fig. 3B). The present distribution of the parasitoids extends beyond these areas in the north, but is restricted in the south (Fig. 1). Areas of New Zealand with similar mean January (the warmest month) temperatures to Canberra (20.7°C) and Melbourne (19.9°C) include those in the Bay of Plenty. Hobart's mean January temperature (16.3°C) falls within the mean summer temperature range of 16-18°C, which is comparable to temperatures found in the west and southern North Island and northern and central South Island (Fig. 3C). The present distribution of the parasitoids covers the North Island areas, but is again restricted in the south (Fig. 1).

Mean annual rainfall levels in Canberra (632 mm), Melbourne (691 mm) and Hobart (668 mm) (Gentilli, 1971) are lower than those found in much of New Zealand (Garnier, 1958). The rainshadow area of South Island's east coast, which is presently beyond the parasitoids' distribution, is the only region of New Zealand that has an annual mean rainfall within the range found at collection sites in Australia (Fig. 3D). Low rainfall does not appear to have been critical for parasitoid establishment. Tasmania, in general, is climatically similar to the South Island of New Zealand (Dwyer, 1958), where a high proportion of the annual rainfall occurs outside the winter months. Seasonally, Canberra, Melbourne and Hobart receive most rain in spring (Dwyer, 1958; Gentilli, 1971), a pattern similar to western Nelson region of the South Island and eastern-central areas of the North Island (Garnier, 1958).

Mean daily temperature ranges are listed in Table 1 for the Australian collection sites and some of the locations where *X. rhopaloceros* and *T. brevifacies* were released in New Zealand.

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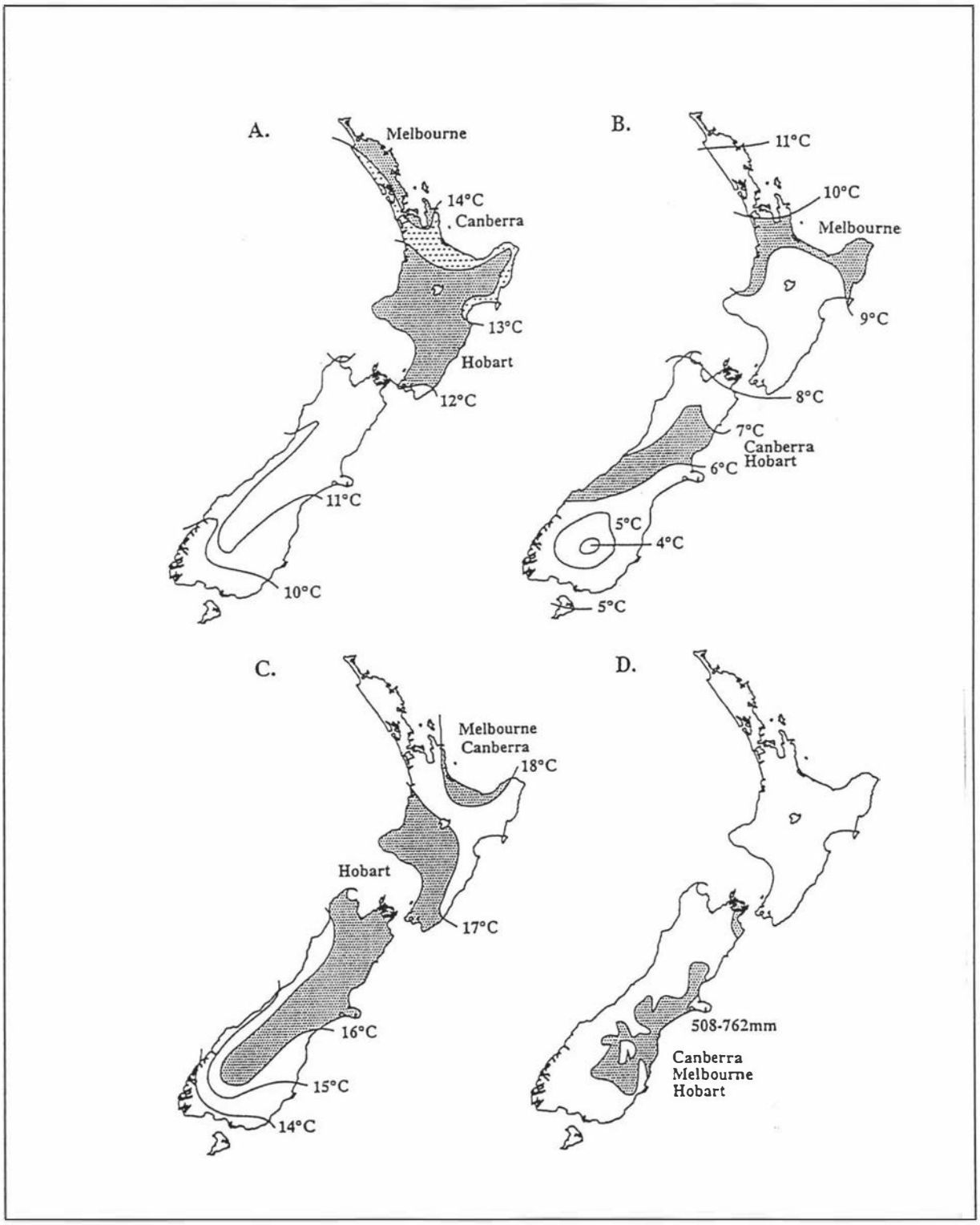

Figure 3. Climate data for areas of New Zealand with climatic features within the range experienced in Canberra, Melbourne and Hobart are illustrated. Climatic features compared include: (A) mean annual temperature; (B) mean July temperatures (midwinter); (C) mean January temperatures (midsummer); (D) mean annual rainfall.

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Frosts are a feature of the New Zealand climate when anticyclones occur in winter (Garnier, 1958), particularly in southern areas (Table 1). Frosts occur in winter in all areas of Victoria except in coastal regions. In Tasmania, heavy frosts occur from autumn to spring (Dwyer, 1958) and Canberra experiences nights below 0°C frequently in winter (Gentilli, 1972).

Mean humidity levels in Canberra, Melbourne and Hobart, expressed as a percentage of relative humidity at 0900h, are highest in winter ranging from 75-81 %; relative humidity is lowest in summer (Gentilli, 1971). This pattern is the inverse of the New Zealand situation where generally humidity levels are highest in February (late summer) and lowest in July (mid winter) (Maunder, 1971).

Table 1. Comparison of climatic data for locations where *X. rhopaloceros* and *T. brevifacies* were collected in Australia and where the parasitoids were released in New Zealand. Data means at sites taken between 70 and 100 years.

Location	Altitude (m)	Mean daily winter temperature Jun-Aug (°C)	Mean daily summer temperature Dec-Feb (°C)	Mean winter ground frosts/month	Mean daily temp range winter (°C)	Mean daily temp range summer (°C)
Canberra	559	6.0-7.4	19.1-20.7	-[a]	9.4-10.9	13.7-14.7
Melbourne	35	9.6-10.5	18.4-19.9	-	7.2-8.3	11.2-11.6
Hobart	53.9	7.8-8.8	15.1-16.3	-	6.4-7.6	9.2-9.7
Auckland[b]	49	10.8-11.8	17.7-19.6	0.6 - 1.7	5.9-6.4	7.1-7.3
Tauranga	4	9.3-10.1	17.0-19.0	11 - 14	9.2- 9.6	9.8-10.3
Napier	2	8.6- 9.6	17.4-18.8	7.7 - 9.1	8.6-9.1	8.8-9.3
Nelson	2	6.4-7.4	15.3-16.9	12 - 21	10.2-10.9	9.4-10.0
Christchurch	7	5.7-6.9	15.4-16.4	17 - 19	8.7-8.8	9.4-9.9

[a] not available
[b] longest standing climate station closest to Kerikeri release site.

Climates suitable for future parasitoid colonisation in New Zealand.

Both parasitoid species are found throughout the North Island. South Island areas predicted to be suitable for colonisation by *X. rhopaloceros* and *T. brevifacies* include those areas climatically similar to the North Island as defined by Garnier (1958) (Figure 4). *Xanthopimpla rhopaloceros* has colonised the Blenheim and Nelson areas in the 'dry', 'moist' and 'humid', warm climate categories and Murchison in the cool climate 'superhumid' category of the Nelson and Blenheim areas.

Other South Island regions that share climate categories with the North Island, but in which neither parasitoid has been recorded, include the 'humid' cool climate areas south of Nelson and the central South Island east of Christchurch, the 'superhumid' cool climate

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region extending from Murchison south along the west coast, the 'moist subhumid' warm climate area of coastal Blenheim, similar to Napier, and the 'superhumid' warm climate areas north-east and north-west of Nelson. Climatically these areas appear suitable for establishment of both *X. rhopaloceros* and *T. brevifacies*.

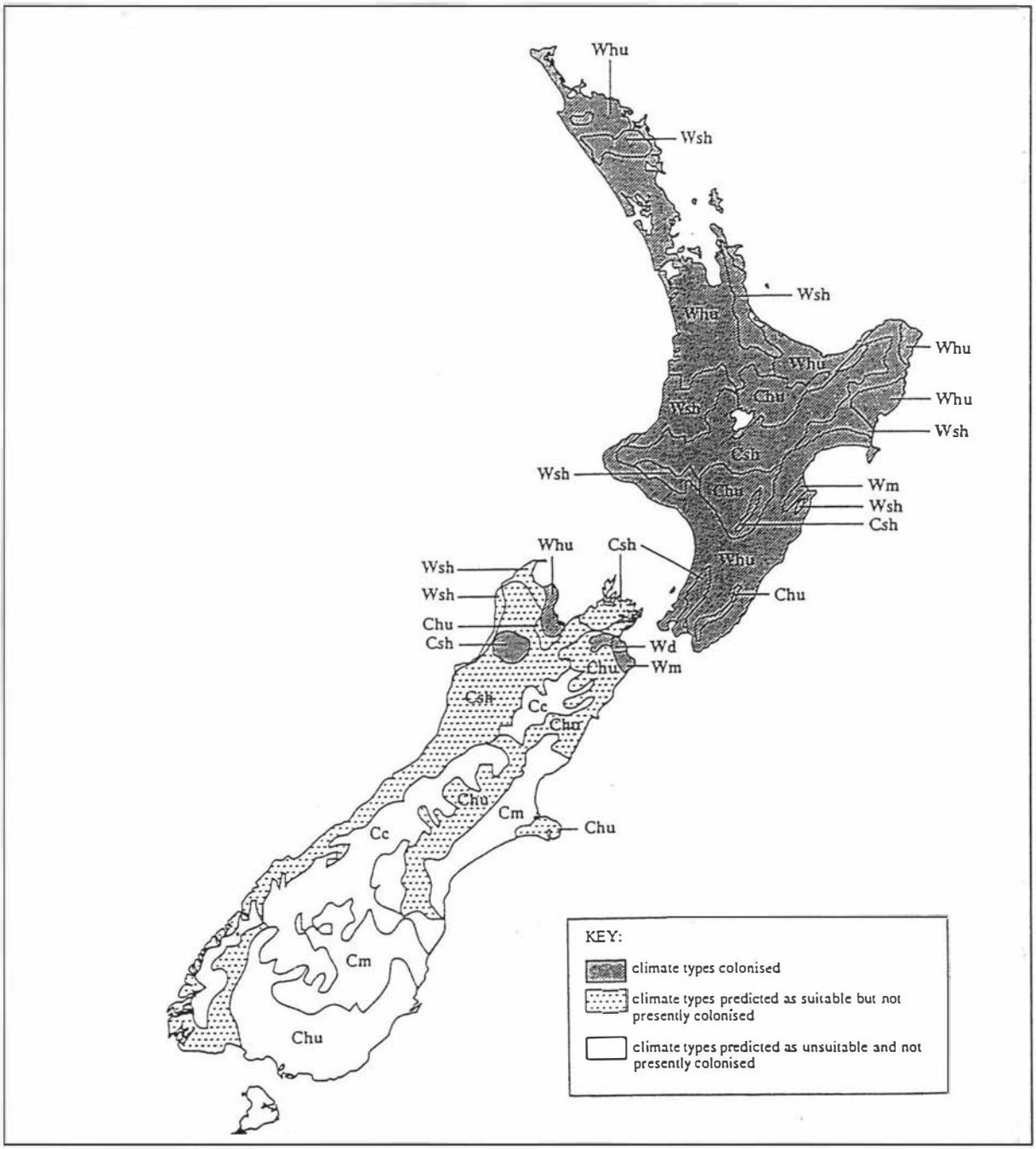

Figure 4. Categories of new Zealand climate types colonised by *X. rhopaloceros* and *T. brevifacies* and South Island regions with climate types that may be colonised by *X. rhopaloceros* and *T. brevifacies*. Climate categories are defined as: Wsh = warm climate, superhumid; Whu = warm climate, humid; Wm = warm climate, moist; Wd = warm climate, dry; Csh = cool climate, superhumid; Chu = cool climate, humid; Cm = cool climate moist; CC = cold climate; Cd = cool climate, dry (categories after Garnier, 1958).

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DISCUSSION

Collection of quantitative data detailing the establishment of the founder populations of *X. rhopaloceros* and *T. brevifacies* was sporadic, apart from the National Leafroller Survey in the 1970s (Wearing, 1994). Therefore, an understanding of the parasitoids' present geographical ranges in New Zealand can be only partially determined by looking retrospectively for associations between them and climate types, hosts, and habitats using data from New Zealand and Australia.

Dispersal.

Establishment of the parasitoids was less successful in the South Island than in North Island areas. Two *T. brevifacies* were collected in Nelson, South Island in 1998, after several releases in the last 29 years (Munro, 1998). It is assumed that these colonists arrived by wind dispersal. If *T. brevifacies* dispersal is assisted by wind, as suggested by Early (1995), a north-east or due east wind is necessary to help disperse the fly to the South Island without further human intervention. The mean annual percentage frequency of easterly winds in Wellington is 1.4 % while north-easterlies occur at a frequency of 3.2 % per annum (Garnier, 1958). If further *T. brevifacies* are able to disperse between North and South Islands, a distance of 25 km, despite the low frequency of suitable north-east and easterly winds, then this species should not be climatically limited when invading the northern South Island. The fly already occurs in climate types in the North Island similar to those available in the northern South Island.

Xanthopimpla rhopaloceros established at Nelson for a short period during the late 1960's after its release, and then disappeared (W.P. Thomas, personal communication, 1996.). It was not seen in the Nelson area for another 20 years, when it was detected in 1989 at Nelson and Blenheim. W.P. Thomas (pers. comm., 1996) suggested that re-establishment of a South Island population of *X. rhopaloceros* was effected by natural dispersal across Cook Strait from southern North Island, rather than from a remnant population remaining undetected in the Nelson area for 20 years.

Xanthopimpla rhopaloceros and *T. brevifacies* have dispersed up to 20 and 58 km respectively across open water to offshore islands (Early, 1995; Munro, 1998) (Fig.1). Therefore, it is conceivable that further offshore islands above latitude 42° S, with a

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population of suitable lepidopteran hosts and within the known dispersal range of 20-58 km, may be colonised by *T. brevifacies* and *X. rhopaloceros*.

Parasitoids used as biological control agents have been recorded dispersing long distances in short periods of time in several post-release monitoring programs. Godfray (1994) documented an instance of a tachinid parasitoid establishing 100 km from its release site one year later. *Xanthopimpla rhopaloceros* dispersed through the length of the North Island of New Zealand in 14 years, radiating away from its 5 release sites at an estimated rate of 19.2 km/year. *T. brevifacies* was first recorded at the southern tip of the North Island in 1988 (Munro, 1998), 21 years after the initial releases were made at 4 North Island locations.

Entomologists have observed at a number of locations that high initial numbers of *X. rhopaloceros* were soon followed by a decline. Several mechanisms could account for this. The population may have reached a lower equilibrium level, a decline in leafroller host numbers may have occurred, or there may have been competition within the leafroller parasitoid guild. Field data from the present study showed that potential parasitoid competitors of *X. rhopaloceros* included the native species *Pales funesta* (Hutton) (Tachinidae) and *Carria fortipes* Cameron (Ichneumonidae), as well as the introduced *T. brevifacies*. Wearing *et al.* (1991) indicated that *Glabridorsum stokesii* Cameron (Ichneumonidae) and *Dolichogenidea tasmanica* Cameron (= *Apanteles tasmanicus* Cameron) (Braconidae) are also part of the parasitoid complex associated with leafrollers. These species parasitise leafroller larvae and pupae (Early, 1984). Thus, parasitoids of earlier sub-imago tortricid stages could limit the number of pupae available for *X. rhopaloceros* oviposition. Ehler and Hall (1982) reported an inverse relationship between rate of establishment by biocontrol agents and the number of established species within the same feeding guild already present in a system. Possible exclusion of *X. rhopaloceros* by *T. brevifacies* (or a combination of other species) is also supported by predictions made in models of intra-guild parasitoid competition (Briggs, 1993), in which parasitoids that oviposit on earlier life stages out-compete species whose hosts are later life stages. Intra-guild competition from egg and larval parasitoids may explain the observed decline in *X. rhopaloceros* abundance, but this remains to be investigated.

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Climate.

The ecotypes of *T. brevifacies* and *X. rhopaloceros* chosen for release in New Zealand may have influenced their pattern of establishment. Goldson *et al.* (1994) highlighted the practice of introducing multiple ecotypes of insect biological control agents to confer a greater chance of establishment and dispersal. This is of particular importance when target pest species occupy several climatic types. Likewise a factor contributing to the establishment of *T. brevifacies* and *X. rhopaloceros* in New Zealand could have been their extensive distributions in Australian ecotypes. Given the wide latitudinal (28° S to approximately 43° S) occurrence of *T. brevifacies* and *X. rhopaloceros* in Australia (Townes & Chiu, 1970; P. Cranston, personal communication, 1996), there was potential for both parasitoids to expand their distribution into all climatically-similar regions of New Zealand that also fulfill their other ecological requirements. The south-eastern Australian and Tasmanian parasitoid ecotypes chosen for release in New Zealand have established predominantly in climatically similar areas in New Zealand during the last 29 years. *X. rhopaloceros* and *T. brevifacies* are now entering South Island areas climatically dissimilar from those at its Australian collection sites.

Ross *et al.* (1982) considered levels of humidity and evaporation as a consequence of high or low temperature to be the most likely factor to limit the geographical range of insects. New Zealand data from Gentilli (1971) and Garnier (1958) showed no evidence that Christchurch, an unsuccessful release site, experienced lower annual levels of relative humidity or had higher levels of evaporation than successful North Island or Nelson parasitoid release sites. However, Christchurch is classified as a 'cool-moist climate' region (Garnier, 1958) and is climatically dissimilar to any climate category currently colonised by *X. rhopaloceros* or *T. brevifacies* in New Zealand. Daily temperature range was considered by Fox (1974) to be a more important climatic factor in determining the successful establishment of Australian insects in New Zealand than mean high or low temperatures *per se*. Daily winter temperature ranges at the three Australian collection locations and five of the New Zealand release sites are very similar (Table 1). Christchurch is cool in winter, with low daily mean winter temperatures and a smaller mean daily winter temperature range than those regions currently colonised by the parasitoids (Gentilli, 1971). These climatic features may have

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contributed to the failure of *X. rhopaloceros* and *T. brevifacies* to establish at Christchurch, as well as the high temperatures and low humidity in summer and spring (Garnier, 1958).

Host range and habitat.

As well as suitable climatic conditions in many areas of New Zealand, the successful establishment of *T. brevifacies* and *X. rhopaloceros* may be a consequence of the wide distribution of their hosts (larval and pupal tortricids) in the North and South Islands (Wearing *et al.*, 1991) and some offshore islands (Dugdale, 1971).The Australian species, *E. postvittana,* is widespread in New Zealand and was the target of this biological control project. The availability of preferred microhabitats may also have aided establishment of *X. rhopaloceros* as with other *Xanthopimpla* species (Townes & Chiu, 1970). It is believed that Tachinidae are more specific to an ecological niche than host specific (B. Cantrell personal communication, 1996). *Trigonospila brevifacies* is presently known to attack 14 lepidopteran species in New Zealand (Munro, 1997) and five species in Australia (Cantrell, 1986).

Australian and New Zealand Tortricidae share a common evolutionary origin (Dugdale, 1977). The co-evolutionary history between *T. brevifacies, X. rhopaloceros* and their Australian tortricid hosts, may have pre-adapted the parasitoids to New Zealand's endemic tortricids. Plant chemicals released when a plant is attacked by phytophagous insects (Turlings *et al.*, 1990) or plant chemicals associated with a specific microhabitat (Vet, 1985; van Alphen *et al.*, 1991) are used by some parasitoids to locate their hosts. It is not known what role, if any, plant chemicals play in the host location behaviour of *T. brevifacies* and *X. rhopaloceros.* However, if experience of plant chemicals allow *T. brevifacies* and *X. rhopaloceros* to locate lepidopteran hosts as has been shown for other parasitoids (Arthur, 1962), then host plant groups that occur in both Australia and New Zealand could have assisted the establishment of these parasitoids in New Zealand. McQuillan (1992) lists the following tortricid food plant families or genera which are native to both New Zealand and Tasmania: *Nothofagus* (Fagaceae). Species of the sub-family Tortricinae feed on *Nothofagus* litter in both Tasmania and New Zealand; Asteraceae, which are fed on by leafroller species from the tribe Archipini, especially by *Epiphyas* sp. in Tasmania and *Planotortrix* sp. in New Zealand; Myrtaceae which occurs in both Australia and New Zealand (Salmon, 1980) and one member, *Leptospermum scoparium* Forster & Forster (tea-tree) hosts a monophagous tortricid in New Zealand (J.S. Dugdale, personal communication, 1996) while several

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Tasmanian Archipini feed on Myrtaceae species; ferns are fed on by monophagous tortricids in both Tasmania and New Zealand (McQuillan, 1992); and tortricids have been recorded on Pittosporaceae in both countries (J.S. Dugdale, unpub.data; McQuillan, 1992). With the presence of these native plant groups and tortricid fauna in common, it is perhaps not surprising that *T. brevifacies* and *X. rhopaloceros* have invaded some native habitats in New Zealand.

The tortricid parasitoids *X. rhopaloceros* and *T. brevifacies* have established in all North Island commercial fruit growing regions and are commonly found where insecticide use is limited. For example, at times *T. brevifacies* parasitises up to 60 % of late instar tortricid larvae on kiwifruit near Tauranga (C. McKenna, personal communication, 1996). The potential of *T. brevifacies* and *X. rhopaloceros* in integrated pest management systems for tortricid pests in fruit crops is being investigated in New Zealand. However, there is some concern that both parasitoids attack native lepidopteran species within the native habitats which they have invaded (Green, 1984; Roberts, 1986; Berry, 1990). Therefore, the occurrence of *X. rhopaloceros* and *T. brevifacies* in native habitats and the parasitism of non-target species warrants further research and quantification of these impacts.

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REFERENCES

Arthur, A.P. (1962) Influence of host tree on abundance of *Itoplectis conquisitor* (Say), a polyphagous parasite of the European pine shoot moth *Rhyacionia buoliana* (Schiff). *Canadian Entomologist* **94**, 337-347.

Berry, J.A. (1990) Two parasitoid complexes: *Hierodoris atychiodes* (Lepidoptera: Oecophoridae) and *Icerya purchasi* (Homoptera: Margarodidae). *New Zealand Entomologist* **13,** 60-62.

Briggs, C.J. (1993) Competition among parasitoid species on a stage-structured host, and its effect on host suppression. *American Naturalist* **141**, 372-396.

Cantrell, B.K. (1986) An updated host catalogue for the Australian Tachinidae (Diptera). *Journal of the Australian Entomological Society* **25**, 255-265.

Crosskey, R.W. (1973) A conspectus of the Tachinidae (Diptera) of Australia, including keys of the supraspecific taxa and taxanomic and host catalogues. *The British Museum (Natural History) Entomology* Supplement **21**, 1-221.

Cordingley, C.L & Danthanarayana, W. (1976) The lepidopterous fauna of capeweed *Arctotheca calendula*) in Victoria with keys for larval identification. *Journal of the Australian Entomological Society* **15,** 19-34.

Danthanarayana, W. & Farrugia, D. (1977) Studies on the biology and systematic position of a new species of ichneumonid parasitising the light brown apple moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae), in Australia. *Bulletin of Entomological Research* **67,** 607-617.

Dugdale, J.S. (1971) Entomology of the Aucklands and other islands south of New Zealand: Lepidoptera, excluding non-crambine Pyralidae. *Pacific Insects Monographs* **27**, 55-172.

Dugdale, J.S. (1977) Some characteristics of phytophagous insects and their hosts in New Zealand. *The New Zealand Entomologist* **6**, 213-221.

Dwyer, L.J. (1958) Fifty years of weather 1908-1957 in the Australian States. Commonwealth Bureau of Meteorology, Australia.

Early, J.W . (1984) Parasites and predators, in *New Zealand pest and beneficial insects* (Scott R.R., Ed). Lincoln University College of Agriculture, Canterbury, New Zealand, pp. 271-308.

Early, J.W. (1995) Insects of the Aldermen Islands. *Tane* **35,** 1-14.

Ehler, L.E. & Hall, R.W. (1982) Evidence for competitive exclusion of introduced natural enemies in biological control. *Environmental Entomology* **11**, 1-4.

Biocontrol Science and Technology 1998, Vol. 8, 559-571.

Fox, K.J. (1974) Trans-oceanic dispersal of insects in New Zealand. *New Zealand Entomologist* **5,** 240-243.

Garnier, B.J. (1958) *The climate of New Zealand.* Edward Arnold Ltd, London, U.K.

Gentilli, J. (1971) *Climates of Australia and New Zealand.* World Survey of Climatology, Vol 13. Elsevier publishing company, London, U.K.

Gentilli, J. (1972) *Australian climate patterns.* Thomas Nelson Ltd, Melbourne, Australia.

Green, O.R. (1984) New Zealand host and locality records for an introduced tortricid parasite, *Trigonospila brevifacies* (Diptera: Tachinidae). *New Zealand Entomologist* **8,** 69-71.

Godfray, H.C.J. (1994) *Parasitoids: behavioral and evolutionary ecology.* Princeton University Press, Princeton, USA.

Goldson, S.L., McNeill, M.R., Proffitt, J.R., Barker, G.M., Addison, P.J., Barratt, B.I.P. & Ferguson, C.M. (1994) Systematic mass rearing and release of *Microctonus hyperodae* (Hymenoptera: Braconidae), a parasitoid of the Argentine stem weevil *Listronotus bonariensis* (Coleoptera: Curculionidae) and records of its establishment in New Zealand. *Entomophaga* **34,** 527-536.

Hailemichael, Y., Smith, J.W. & Wiedenmann, R.N. (1994) Host finding, host acceptance and host suitability of the parasite *Xanthopimpla stemmator. Entomologia Experimentalis et Applicata* **71,** 155-166.

Kapadia, M.N. (1987) Occurrence and distribution of different parasites of *Opisina arenosella* under Mahuva conditions of Gujarat. *Gujarat Agricultural University Research Journal* **12,** 17-21.

Kfir, R. (1991) Selecting parasites for biological control of lepidopterous stalk borers in summer grain crops in South Africa. *Redia* **74**, n. 3 appendices, 231-236.

Kfir, R. (1994) Attempts at biological control of the stem borer *Chilo partellus* (Lepidoptera: Pyralidae) in South Africa. *African Entomology* **2,** 67-68.

Maunder, W.J. (1971) Elements of New Zealand's climate, in *Climates of Australia and New Zealand* (Gentilli, J., Ed). World Survey of Climatology, vol 13. Elsevier publishing company, London, U.K, pp. 229-261.

McQuillan, P.B. (1992) A checklist of the Tasmanian tortricid moths (Lepidoptera: Tortricidae) and their host-plant relationships. *Papers and Proceedings of the Royal Society of Tasmania* **126**, 77-89.

Biocontrol Science and Technology 1998, Vol. 8, 559-571.

Munro, V.M.W. (1997) *Eutorna phaulocosma* Meyrick (Lepidoptera: Oecophoridae), a new host for the introduced Australian parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae). *New Zealand Entomologist* **20**: 71-72.

Munro, V.M.W. (1998) A record of the releases and recoveries of the Australian parasitoids, *Xanthopimpla rhopaloceros* (Ichneumonidae) Krieger and *Trigonospila brevifacies* (Hardy) (Tachinidae), introduced to New Zealand for leafroller control. *New Zealand Entomologist* **21** (in press).

Naumann, I.D. (1991) Hymenoptera, in *The Insects of Australia: a textbook for students and research workers* (Naumann, I.D., Ed). CSIRO Entomology Division, Canberra Australia, pp. 916-1000.

Pillai, G.B. & NAIR, K.R. (1989) Observations on *Xanthopimpla punctata punctata* (Hymenoptera: Ichneumonidae), a pupal parasitoid of *Opisina arenosella*. *Journal of Plantation Crops* **16**, 173-177.

Pillai, G.B. & NAIR, K.R. (1990) Role of ichneumonid parasitoids in the biological suppression of the coconut leaf eating caterpillar, *Opisina arenosella*. *Indian Coconut Journal* **21,** 3-10.

Roberts, L.I.N. (1986) The practice of biological control - implications for conservation, science and community. *The Weta* **9,** 76-84.

Ross, H.H., Ross, C.A. & Ross, J.R.P. (1982) *A Textbook of Entomology*. John Wiley & Sons, New York USA.

Salmon, J.T. (1980) *The native trees of New Zealand*. Reed Books, Auckland, New Zealand.

Sankaran, T. & Syed, R.A. (1972) The natural enemies of bagworms on oil palms in Sabah, East Malaysia. *Pacific Insects* **14,** 57-71.

Singh, S.P. (1992) Frequent outbreaks of *Cricula trifenestra* (Lepidoptera: Saturnidae) on mango. *Indian Journal of Plant Protection* **20,** 114-115.

Sran, C.S & Sandhu, G.S. (1979) New records of parasites and predators of *Nephopteryx eugraphella* in India. *Current Science* **48,** 169.

Townes, H. & Chiu, S-C. (1970) The indo-Australian species of *Xanthopimpla* (Ichneumonidae). *Memoirs of the American Entomological Society* **14,** 1-372.

Thomas, W.P. (1989) *Epiphyas postvittana*, the lightbrown apple moth, in *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 187-195.

Biocontrol Science and Technology 1998, Vol. 8, 559-571.

Turlings, T.C.J., Tumlinson, J.H. & Lewis, W.J. (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* **250**, 1251-1253.

van Alphen, J.J.M., Nordlander, G. & Eijs, I. (1991) Host habitat finding and host selection of the *Drosophila* parasitoid *Leptopilina australis* (Hymenoptera, Eucoilidae) with a comparison of the niches of European *Leptopilina* species. *Oecologia* **87**, 324-329.

Vet, L.E.M. (1985) Olfactory microhabitat location in some eucoilid and alysiine species (Hymenoptera), larval parasitoids of Diptera. *Netherlands Journal of Zoology* **35**, 486-496.

Wang, W.X. & Liu, W.Q. (1994) Field surveys on the pupal parasitism of *Dendrolimus punctatus* (Lepidoptera: Lasiocampides) in Guangxi and Hunan. *Chinese Journal of Biological Control* **9,** 143-144.

Wearing, C.H., Thomas, W.P., Dugdale, J.S. & Danthanarayana, W. (1991) Tortricid pests of pome and stone fruits, Australian and New Zealand species, in *Tortricid Pests, Their Biology, Natural Enemies and Control* (van der Geest, L..P.S. & Evenhuis, H.H., Eds). Elsevier Science Publishers B.V, Amsterdam, The Netherlands. pp 453-472.

Wearing, C.H. (1994) National Leafroller Survey: Species Distribution Charts for Crops and Regions. *HortResearch Internal Report No. IR 94-64* pp 51.

Williams, J.R. (1983) The sugar cane stem borer (*Chilo sacchariphagus*) in Mauritius. *Revue Agricole et Sucriere de I'lle Maurice* **62,** 5-23.

The host range of the introduced Australian parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) in New Zealand: when, which and how non-target Lepidoptera are parasitised.

ABSTRACT

Archival records and field-collected data from the present study show that *Trigonospila brevifacies* has been reared from 17 host lepidopteran species in five families since its introduction to New Zealand thirty years ago. However, most archival host records are from urban areas. In native forests, the number of hosts attacked by *T. brevifacies* is significantly fewer at nine species from two families. Five of these native species parasitised by *T. brevifacies* are minor or major pests in fruit crops. Parasitism levels and abundance of host species are positively related and this may account for the disparity between the types of host attacked by *T. brevifacies* in urban areas compared to native forests in New Zealand.

In some parasitoid species experience of hosts as juveniles influences which host species the adult will choose to oviposit. Pre-imaginal exposure of *T. brevifacies* to host odours did not affect host selection by adult females.

Connectance webs of plant-host-parasitoid trophic relationships in native forests showed that *T. brevifacies* oviposited on lepidopteran species collected from 20 species of plant in 18 genera, and it is therefore unlikely that specific plant chemicals are used as host finding cues by this parasitoid. The most frequently parasitised plant-host combination was the endemic tortricid *C. obliquana* collected from the tree *Melicytus ramiflorus* Forster (F: Violaceae).

The host characteristic that defines *T. brevifacies'* host range of phylogenetically diverse lepidopteran species is that all hosts so far recorded have a common feeding niche, they are concealed feeders using vegetal structures of shoots, leaves or flower buds. The mechanism by which *T. brevifacies* larvae are able to overcome the immune defense systems of this diverse group of hosts is the adaptation of a respiratory tube.

INTRODUCTION

Trigonospila brevifacies (Hardy) (Diptera: Tachinidae) was introduced to New Zealand as one of a suite of biological control agents against the Australian orchard pest tortricid *Epiphyas postvittana* (Walker) in the late 1960s and early 1970s (Thomas, 1989). Archival

records from the 1950s and 1960s held at the C.S.I.R.O, Canberra indicate that *T. brevifacies* was documented as a polyphagous parasitoid and not host specific to *E. postvittana* in Australia (Munro, unpub.data). This lack of host specificity was not predicted by the workers introducing this biological control agent to New Zealand in the late 1960s (Cameron *et al.*, 1993), but host specificity was not a prerequisite for the introduction of *T. brevifacies*. When the first instances of *T. brevifacies* attacking non-target hosts were recognised in the mid-1970s, the hosts were native-pest Tortricidae occurring in orchards (Wearing, 1994) and this outcome was thus considered advantageous. At the time of *T. brevifacies* release in New Zealand, polyphagy was viewed by biocontrol practitioners as a useful characteristic in entomophagous biological control agents in certain conditions (Cameron *et al.*, 1993). Polyphagy assists establishment in new geographical locations at times when the target host is temporarily unavailable (Grenier, 1988) and increases the likelihood of a parasitoid surviving in a reservoir area inhabited by alternative hosts, and hence it's ability to re-invade fruit crops during the target host's next generation (Cameron et al., 1993).

Since the era when *T. brevifacies* was introduced to New Zealand, more value has been attached to native ecosystems and to all faunal components important to the functioning of these systems. The Animals Amendment Act 1990 and the Hazardous Substances and New Organisms Act 1996 now provide a framework in which judgments can be made about the suitability of biological control agents proposed for introduction to New Zealand. Although a balance between economic benefits and environmental risks were considered historically when making irreversible introductions of biological control agents, a wider range of potential risks to organisms of environmental and cultural value are now to be considered under the HSNO Act (1996).

Wearing (1994) documented the attack of non-target native pest Tortricidae in orchards during the mid-1970s. Green (1984) listed a group of non-target and non-tortricid native hosts from urban and orchard environments parasitised by *T. brevifacies* in New Zealand. Roberts (1986) highlighted the potential risks posed by *T. brevifacies* to native habitats and its attack of non-target native species. However, no quantitative work had been carried out in native habitats to determine the circumstances under which non-target native Lepidoptera were attacked by *T. brevifacies*. Thus an examination of *T. brevifacies* host range in native New Zealand habitats was required. Five aspects related to *T. brevifacies* host range were chosen for study to gain an understanding of when non-target hosts are attacked, to define the types of Lepidoptera that could be attacked, and to identify

the biological mechanism that allows *T. brevifacies* to reproduce on such a broad range of hosts.

The five areas discussed in this chapter include: phylogenetic and behavioural similarities of the hosts parasitised; the role of host-plant associations and the hosts attacked; the relationship between host abundance and levels of parasitism; identification of temporal or spatial patterns within the lepidopteran host community; and whether pre-imaginal conditioning influences ovipositional behaviour in *T. brevifacies*.

METHODS

Study sites

The host range of *T. brevifacies* was surveyed at six sites of mature broadleaf/podocarp forest in three North Island entomological regions (Bay of Plenty, Wanganui and Wairarapa) as defined by Crosby *et al.*, (1976). Two replicate sites of similar forest composition, climate and altitude were chosen in each region to determine whether patterns recorded in the host community and *T. brevifacies* behaviour were consistent within regions and seasons.

The Bay of Plenty sites were located at 300 m a.s.l between Lake Rotoehu and the Rotoehu Forest of exotic *Pinus radiata* Don at (176° 31'E, 37° 56'S) and (176° 31'E, 37° 58'S). The Wanganui sites were located at Totara Reserve (175° 49'E, 40° 11'S) (305 m a.s.l) north of Palmerston North and at Bushy Park (174° 56'E, 39° 49'S) (280 m a.s.l) north-west of Wanganui. The Wairarapa sites were located at Tane (175° 52'E, 40° 70'S) (320 m a.s.l) south-east of Pahiatua and Mt. Bruce (175° 36'E, 40° 40'S) (600 m a.s.l) north of Masterton.

Field sampling

Potential lepidopteran hosts were sampled from each of the six study sites on seven occasions over a two year period. On each sampling occasion two forty-metre transects were chosen. Lepidopteran larvae and host plants were sampled at 2 metre intervals along each transect. Plants were searched from ground level to approximately 2 m high, one caterpillar was taken from the nearest plant to the transect. If no larvae were detected after searching the plant closest to the transect the next nearest plant to the transect was searched. Forty larvae were taken on each occasion per site. The time taken to collect forty larvae per sampling occasion was recorded and used as a measure of host abundance.

Collected larvae were transferred to vials of general purpose diet (Singh, 1983) in a controlled temperature (18°C ± 2°C) and light (LD: 16/8) laboratory. Larvae and host plants were identified to species, instar stage noted and the number and position of any *T. brevifacies* eggs were recorded. Each larva was assigned a code and emergences of parasitoids and adult Lepidoptera were noted during daily inspections.

Host identification

All collected larvae were identified using unpublished keys provided by J.S. Dugdale (Landcare Research, Nelson) who also verified host identifications. Adult moths that emerged from field collected larvae were retained to check the validity of larval identification. Lepidopteran larval cadavers, or the remains of *T. brevifacies* puparia where host species could not be identified by other means, were identified using molecular methods. Specimens were sent to Lincoln University for identification using restriction length polymorphism (RFLP) detected in PCR amplified rDNA (Armstrong *et. al.*, 1997).

Laboratory experiment

The effect of pre-imaginal conditioning in *T. brevifacies* was investigated in a controlled temperature (18°C ± 1°C) and light (LD: 16/8) environment. A colony of *T. brevifacies* was founded from wild individuals, and eight generations of *T. brevifacies* were reared on the endemic tortricid *Ctenopseustis obliquana* Walker. Emerging eighth generation females were each retained in individual cages (cylindrical clear plastic Click Clack ™ food container 30 cm by 24 cm) and provided with wet cotton wool and a honey-agar diet. Two emerging *T. brevifacies* males were introduced to each female's cage.

After each female exceeded the mean pre-ovipositional period of seven days (Chapter 5) they were released individually into a secure laboratory (24 m^2 floor space). Eighteen two-metre high potted 'Royal Gala' apple trees were arranged in six rows of three trees. Three tortricid species, the two native species *C. obliquana* and *Planotortrix octo* Walker and the self-introduced pest *E. postvittana*, were made available to *T. brevifacies* for oviposition. Three late-instar larvae from one species were placed on each tree into shelters where two leaves were pinned together. Hosts were arranged in a Latin square design on the trees where three larvae from the three species were randomly assigned to a tree in each row. Thus 18 individuals from each species were made available to each female in groups of three in six rows.

Each female was exposed to this regime for a twelve hour period and then re-captured. Larvae and their associated shelters were then removed from the trees and the number of larvae parasitised from each host species was counted.

Data analysis

The relationship between host abundance and both frequency and / or percentage parasitism by *T. brevifacies* in the field was initially analysed using the Pearson Correlation in SYSTAT (Wilkinson *et. al.*, 1996). The analysis was repeated after excluding rare host species to see if a significant trend held. The data were also analysed (as above) where cases of host species receiving zero parasitism were removed from the data set. Because the trend for greater percentage parasitism on most abundant host species became non-significant when instances of zero parasitism were removed a T-test was performed on the data. The T-test data were grouped into the abundance of parasitised species versus the abundance of non-parasitised species.

The propensity for *T. brevifacies* to oviposit on a host of a different species to that on which it was reared in the laboratory was investigated by testing for interactions between the frequency of parasitism, individual female ovipositional preferences and host species. Sample sizes were too small for a loglinear model to be used for analysis. Therefore, initially a global test of homogeneity was performed using 3-way tables in Chi-Square (SYSTAT). As half the expected frequencies were < 4 the result was not reliable. A loglinear model was then used to test for the interaction term. No 3-way interaction was detected but, as the sample size was small, differences were detected between the Pearson and Likelihood Ratio Chi-Square statistics. However, as there was no deviation from homogeneity (indicated by the small expected frequency) and as the design of the experiment was balanced, it was appropriate to use the process of collapsability. The 3-way tables were collapsed into sets of 2-way tables, thus gaining statistical power (Freeman, 1987). Thus, the factors of female and host species were tested in 2-way Chi-Square tables for effects on parasitism rates.

Spatial and temporal patterns within and between lepidopteran host communities and the frequency of *T. brevifacies* parasitism in native forests were explored using the ordination analysis DECORANA in PC-ORD (McCune, 1987). The Multiple Response Permitation Procedure (MRPP) was performed with SYSTAT to test whether the variability in site and seasonal patterns of host community composition and parasitism were significant. Both Euclidian and Sorenson distance measures were used in the analysis.

RESULTS

Host records

During the two-year survey of six sites of native forest, 2,000 lepidopteran larvae were collected, and of these, *T. brevifacies* was found to attack eight species from the families Tortricidae and Oecophoridae. Five of these species were new host records (Table 1). Seven of the species recorded are native to New Zealand and five of these are minor or major pests of fruit crops. It is interesting to note that the pest species *E. postvittana,* which *T. brevifacies* was introduced to control, was not recorded as a host of the parasitoid in native habitats.

A search of literature and archival data in New Zealand for previous host records for *T. brevifacies* found that 11 species from the families Tortricidae, Pterophoridae, Oecophoridae, Geometridae, and Gelechiidae were recorded. All but one of the hosts in these records were collected from urban or orchard environments, as prior to the present study no attempt had been made to determine *T. brevifacies* host range in native habitats (Table 1).

Literature and C.S.I.R.O. records in Australia were searched to gain an understanding of the host range of *T. brevifacies* in it's native country. A catalogue of Australian Tachinidae lists a pyralid species and the tortricid *E. postvittana* as hosts of *T. brevifacies* (Cantrell, 1986). Another review documents an oecophorid, a gelechiid and two other tortricid species as hosts of *T. brevifacies* (Crosskey, 1973). Thus, even in its native country *T. brevifacies* has been found to oviposit on only six species from three lepidopteran families (Table 1).

The host species parasitised by *T. brevifacies* in New Zealand are not closely related. Only Oecophoridae and Gelechiidae belong to the same superfamily Gelechioidea. However, a common characteristic shared by the hosts of *T. brevifacies* is that their larvae are all concealed feeders, using vegetation shelters or frass and webbing (Table 1).

Effect of pre-imaginal conditioning on polyphagy

Fifteen adult female *T. brevifacies* were tested individually for their ovipositional response to three host species, *C. obliquana, P. octo* and *E. postvittana.* Tested females and seven predescendent generations were reared on *C. obliquana.* Initial analysis of the 3-way table with a loglinear model found no significant association between the three terms, host species (3 levels), parasitism of host and individual female ($\chi^2_{72} = 45.08$, $P=0.99$).

Table 1. Host records for *Trigonospila brevifacies* in New Zealand and Australia.

First record	Host species	Host family	Habitat category	Larval habit	Pest status
New Zealand					
Native habitats Species = 8 Families = 2 (*n* = 2,000) * new record					
Munro 1997 survey	*Apoctena flavescens* (Butler)*	Tortricidae	native	joins leaves	
Munro 1996 ssurvey	*Ctenopseustis obliquana* (Walker)	Tortricidae	native	joins leaves	pest
Munro 1997 survey	*Epalxiphora axenana* (Meyrick)	Tortricidae	native	joins leaves	pest
Munro 1998 survey	*Strepsicrates ejectana* (Walker)*	Tortricidae	native	joins leaves	
Munro 1997 survey	*Planotortrix octo**	Tortricidae	native	joins leaves	pest
Munro 1997 survey	*Planotortrix excessana* (Walker)*	Tortricidae	native	joins leaves	pest
Munro 1997 survey	*Planotortrix notophaea* (Turner)	Tortricidae	native	joins leaves	pest
Munro 1996 survey	*Eutorna phaulocosma* (Meyrick)*	Oecophoridae	native	joins leaves	pest
Archival Species = 11 Families = 5					
Russell 1987	*Grapholita molesta* (Busck)	Tortricidae	orchard	joins leaves	pest
Green 1984	*Ctenopseustis obliquana* (Walker)	Tortricidae	urban	joins leaves	pest
Wearing 1994	*Ctenopseustis obliquana* (Walker)	Tortricidae	orchard	joins leaves	pest
Green 1984	*Epiphyas postvittana* (Walker)	Tortricidae	orchard	joins leaves	pest
Green 1984	*Cnephasia jactatana* (Walker)	Tortricidae	native (scientific reserve)	joins leaves	pest
Green 1984	*Epalxiphora axenana* (Meyrick)	Tortricidae	urban	joins leaves	pest
Wearing 1994	*Planotortrix notophaea* (Turner)	Tortricidae	orchard	joins leaves	pest
Green 1984	*Platyptilia falcatalis* (Walker)	Pterophoridae	urban	burrows into plant structures	
Green 1984	*Heliostibes atychioides* (Butler)	Oecophoridae	urban	webs leaves of native & exotic conifers	
Green 1984	*Pasiphila lunata* (Philpott)	Geometridae	urban	burrows into new shoots	
Green 1984	*Aciptilia monospilalis* (Walker)	Pterophoridae	urban	burrows into plant structures	
Green 1984	*Stathmopoda skelloni* (Butler)	Gelechiidae	orchard	feeds on dead leaf tissue	pest
Australia Species = 5 Families = 4			**Host family**		
Cantrell 1986	*Stericta carbonalis* (Guenee) (= *Epipaschia costigeralis* Walker)		Pyralidae	-	
Cantrell 1986	*Epiphyas postvittana* (Walker)		Tortricidae	joins leaves	pest
CSIRO coll.	*Epiphyas xylodes* (Meyrick)		Tortricidae	joins leaves	pest
Crosskey 1973	*Ageletha hemiteles* (Meyrick) (= *Heliocausta hemiteles* Meyrick)		Oecophoridae	-	
Crosskey 1973	*Phthorimaea operculella* (Zeller)		Gelechiidae	burrow into leaf or tuber	pest

However, when many expected frequencies in the table are < 4, the test is not very reliable. Since the design is balanced and there is no evidence of a 3-way interaction, the 3-way table can be collapsed into sets of 2-way tables (Freeman, 1987).

There was no significant preference for host species (χ^2_2=0.80, P=0.66), nor any variation in parasitism rate among individual females (χ^2_{14}=12.20, P=0.59). Therefore, pre-imaginal conditioning does not appear to limit host choice by adult female *T. brevifacies*, at least within the family Tortricidae.

Host-plant relationships

During the two year North Island survey, data were also gathered on the species of plant from which hosts of *T. brevifacies* were collected. These data were used to investigate whether *T. brevifacies* chooses its hosts on the basis of the plant host rather than the species of lepidopteran.

Figure 1 illustrates these plant-host-*T. brevifacies* relationships where data are aggregated temporally (combining seasons) and spatially (combining sites) in a semi-quantitative trophic connectance web. Larvae parasitised by *T. brevifacies* were collected from 20 plant species in 19 genera and 18 families including Angiosperms, Gymnosperms and even ferns. Therefore, it appears the host range of *T. brevifacies* is not defined by the group of plants on which its lepidopteran hosts feed.

Although hosts feeding on some plant species were more frequently parasitised by *T. brevifacies* this was a reflection of caterpillar abundance on these plant species, rather than a link between *T. brevifacies* parasitism and plant characteristics *per se*. Hosts were most frequently parasitised on mahoe (*M. ramiflorus*) with 30% of all ovipositions recorded on this plant. Twenty percent of parasitised hosts were found on blackberry (*Rubus fruticosus* L.agg.) and 10 % of hosts were collected from tawa (*Beilschmiedia tawa* A. Cunn.). The most frequent plant-host combinations were *Planotortrix* sp. feeding on mahoe, *C. obliquana* feeding on mahoe, *C. obliquana* feeding on tawa and the accidentally introduced pest *Eutorna phaulocosma* Meyrick feeding on blackberry.

Frequency of attack on host species

During the two year survey, the lepidopteran species most frequently parasitised by *T. brevifacies* was the native pest species *C. obliquana* making up 47.6 % of all *T. brevifacies* parasitism recorded. The two *Planotortrix* species were combined for this analysis because the molecular probe for species identification was unable to distinguish between *Planotortrix octo* and *Planotortrix excessana* (Walker). The combined records of *P. octo* and *P. excessana* accounted for 33.2 % of all parasitism, while the remaining five host species made-up only 19.2 % of parasitism recorded (Figure 1).

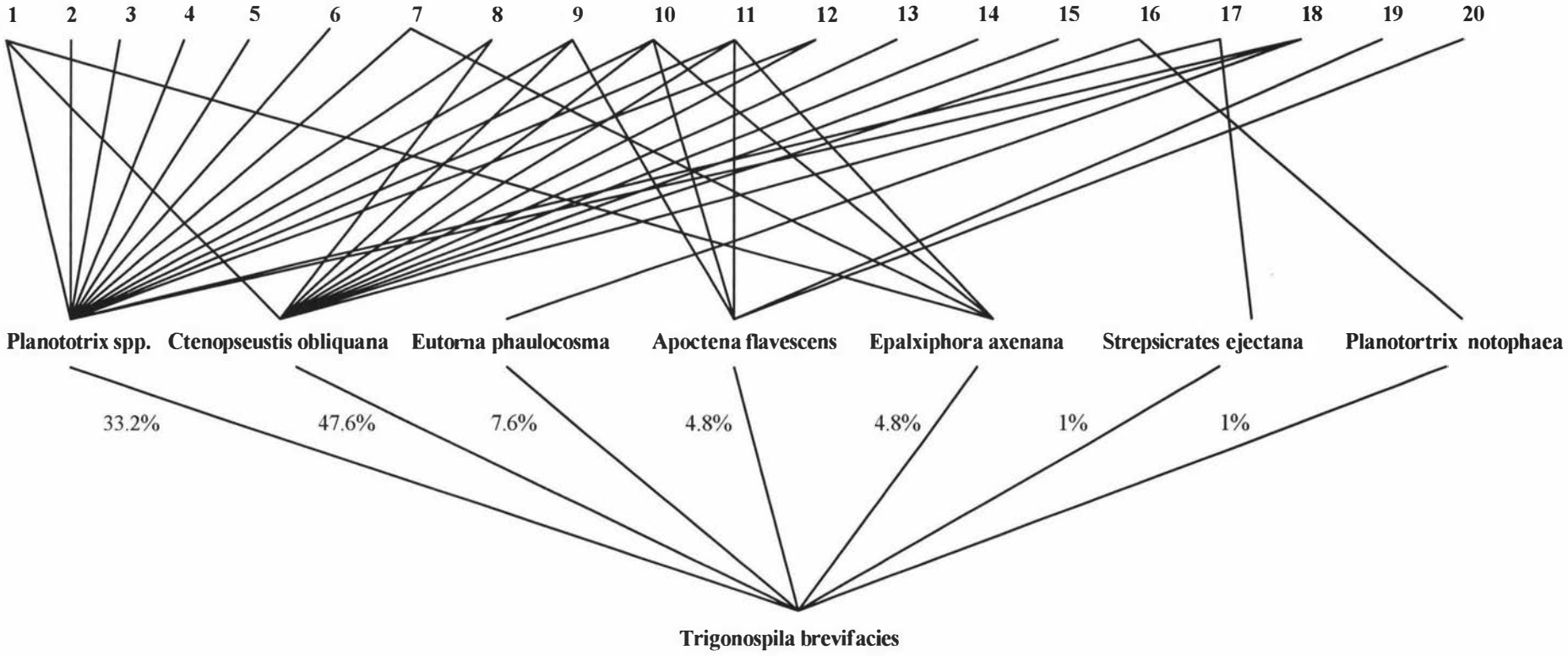


Figure 1. Trophic connectance web of host plants and Lepidoptera parasitised by *Trigonospila brevifacies* in native forests. Level 1: host plants of Lepidoptera; level 2: host Tortricidae and the proportion of *T. brevifacies* diet they represent.

Plant species:

1 fuchsia *Fuchsia exorticata* (F: Onagraceae)
2 fern *Cyclosorus penniger*
3 mapau *Myrsine australis* (F: Myrsinaceae)
4 pukatea *Laurelia novae-zelandiae* (F: Monimiaceae)
5 rangiora *Brachyglottis repanda* (F: Compositae)
6 ribbonwood *Plagianthus regius* (F: Malvaceae)
7 pigeonwood *Hedycarya arborea* (F: Monimiaceae)
8 wineberry *Aristotelia serrata* (F: Elaeocarpaceae)
9 willow *Salix* sp. (F: Salicaceae)
10 kawakawa *Macropiper excelsum* (F: Piperaceae)
11 mahoe *Melicytus ramiflorus* (F: Violaceae)
12 tawa *Beilschmiedia tawa* (F: Lauraceae)
13 rata *Metrosideros umbellata* (F: Myrtaceae)
14 titoki *Alectryon excelsus* (F: Sapindaceae)
15 bush lawyer *Rubus cissoides* (F: Rosaceae)
16 kanono *Coprosma grandifolia* (F: Rubiaceae)
17 miro *Prumnopitys ferruginea* (F: Podocarpaceae)
18 blackberry *Rubus fruticosus* (F: Rosaceae)
19 parconsia *Parsonsia heterophylla* (F: Apocynaceae)
20 putaputaweta *Carpodetus serratus* (F: Escalloniaceae)

The association between the level of parasitism by *T. brevifacies* and the abundance of host species in the field was positive (Figure 2). A series of analyses were conducted to test the validity of this trend. Pearson correlations showed a significant association between host species abundance and both frequency of parasitism (r^2= .592, P <0.005) and percentage parasitism (r^2= .363, P <0.005) by *T. brevifacies*. When the two most rare host species were excluded from the analysis both categories of parasitism were still significant, frequency (r^2= .557, P <0.005) and percentage (r^2= .321, P <0.005). Despite these significant correlations, the trend in Figure 2 is not convincing. This is because there are many overlapping data points, low abundance of a hosts species and zero parasitism.
If these cases with zero parasitism were excluded, the association between frequency of parasitism and host abundance remained significant (r^2= .464, P < 0.002) however, the association between host abundance and percentage parasitism was not (r^2= .184, P = 0.239). A T-test confirmed that if all the records were divided into those with no parasitism, and those with any parasitism there was a significant difference in mean host abundance ($t_{6.369}$ =93, P < 0.001).

Regression lines constructed from seasonal data also indicated a positive trend between parasitism rate and host abundance. Similar rates of *T. brevifacies* parasitism were seen in autumn and summer with lower levels occurring in spring Figure 2. The validity of this trend was statistically tested as follows.

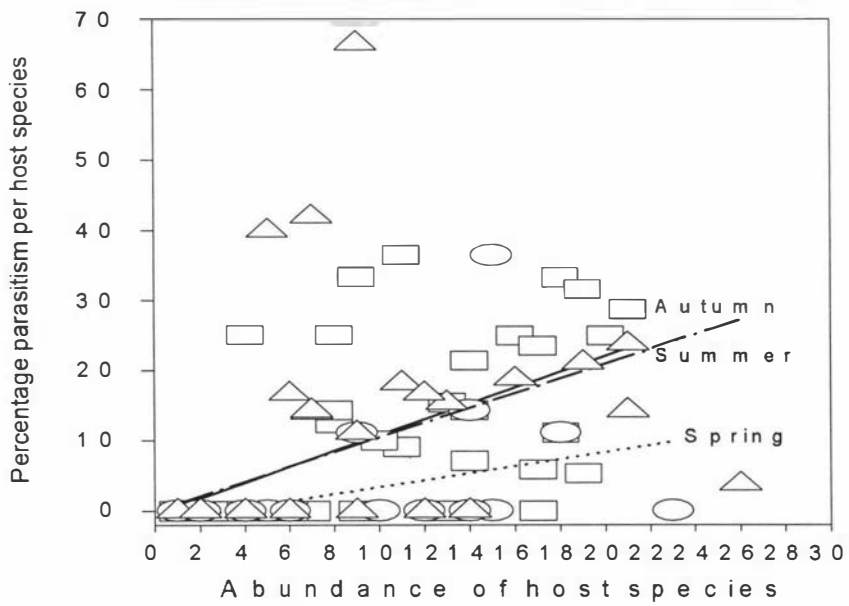


Figure 2. Seasonal host abundance and rate of parasitism. Seasons are represented as; squares = autumn, triangles = summer, circles = spring.

Community patterns

The frequency with which host species were parasitised by *T. brevifacies* and the composition of host communities at each site and in each season was compared using the ordination analysis DECORANA (PC-ORD). The Tane site had the most distinct tortricid community, where high levels of *C. obliquana* coincided with a high frequency of *T. brevifacies* parasitism and *Epalxiphora axenana* Meyrick were rare. These patterns were consistent at this site over the two year sampling period and are shown associated with this site on axis 1 (Figure 3).

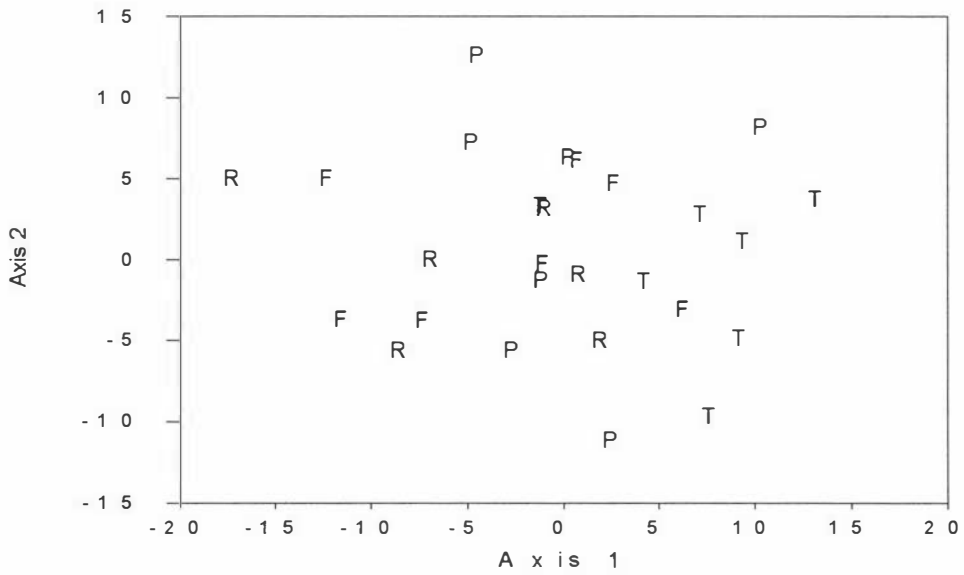


Figure 3. Ordination of frequency of *T. brevifacies* parasitism on host species and the composition of the host community by site using DECORANA. Sites are represented by the following symbols: F = Rotoehu Forest (Bay of Plenty), R = Rotoehu Reserve (Bay of Plenty), P = Pohangina Valley (Manawatu) and T = Tane (Manawatu).

To determine if the patterns found at the Tane site were significant, MRPP analysis was then used to test whether differences in the lepidopteran communities between sites were significant using both the Sorenson's distance measure (R=.121, P=0.001) and a Euclidian distance measure (R=.104, P = 0.002). These results indicate that species most frequently parasitised by *T. brevifacies* were different at different sites. However, there were no seasonal patterns among *T. brevifacies* host communities where certain species may have been consistently abundant at certain times of the year, (R=.104, P = 0.422 Euclidian distance) and (R=.004, P=0.359 Sorenson's distance) distance measures.

DISCUSSION

When and where does non-target parasitism occur

Extensive host range records of the lepidopteran species parasitised by *T. brevifacies* in New Zealand now exist (Green, 1984; Thomas, 1989; Wearing, 1994; Munro, 1997; Munro, unpub data). The species and families recorded as hosts of this parasitoid in urban (mainly Auckland) and orchard environments differ from those found in native forest habitats (see Table 1).

This disparity of host records between urban/orchard and native environments may simply, in some cases, be because some species occur in one habitat but not the other. For example the light brown apple moth, *E. postvittana*, was parasitised by *T. brevifacies* in orchards and urban areas, but was never collected from native forests. The differences between the types of host species parasitised in the two habitat types studied could also be linked to perturbations in population dynamics of target hosts, non-target hosts and the parasitoid. In a review of potential non-target effects of parasitoids, Cullen (1997) predicts that non-target hosts are likely to be attacked following an abundance of target hosts, which allows higher levels of reproduction by the parasitoid and in the ensuing parasitoid generation a spill over of parasitism occurs on to non-target hosts. Anecdotal records from the early 1980s, when *T. brevifacies* was first recorded in Auckland, supports this view. At the same time that *T. brevifacies* was frequently observed it was noted that lepidopteran damage by non-target geometrids to kawakawa hedges declined (J.S. Dugdale, Landcare Research, pers. comm. 1996).

Another aspect of the mechanism outlined by Cullen (1997) was proposed by Jansen (1989) and Belshaw (1994). Jansen (1989) and Belshaw (1994) propose that switching to non-target hosts occurs when the abundance of target host species is low. Strong *et al.*, (1983) define host switching as the addition of a new host to an insects diet or host range. Parasitoid abundance and/or low densities of preferred hosts increases the frequency of accidental encounters with non-target species. Therefore, a parasitoid with what appears to be a wide host range may usually attack only a small group of species, but under the conditions described will parasitise other species outside this group.

The two aspects of this mechanism, spill over and host switching, potentially have different outcomes for non-target species. In a native habitat the spill over effect on to non-target hosts is likely to be transitory. That is, when parasitoid numbers decline in subsequent generations with natural population perturbations non-target hosts will no longer be attacked. However, with host switching if the parasitoid constrains primary host

abundance the impact on secondary hosts may be longer lasting. The behaviour of *T. brevifacies* in native habitats appears to have elements of the host switching model, where the most abundant species spatially and temporally were more likely to be parasitised. As different hosts were more abundant in different seasons and geographical locations, host switching may have occurred. Consequently rare species were the least likely species to be parasitised by *T. brevifacies*.

Defining the host range

Archival records, field surveys and behavioural observations were utilised to construct a general host profile and make predictions of the host characteristics that predispose non-target lepidopterans to the risk of parasitism by *T. brevifacies*.

Environmental and host characteristics are known to link phylogenetically distant species in common parasitoid host ranges. These include host plant (Herrebout, 1969), host shape or host size (Gross, 1993), and microhabitat (Hailemichael, 1994). However, no particular association with macro-habitat, lepidopteran family, or plant group was found to define the host range of *T. brevifacies*. Neither does experience of hosts by parasitoid larvae prevent *T. brevifacies* from switching host species between generations.

Yet, a variety of phylogenetically distant host species share certain characteristics that elicit ovipositional responses in *T. brevifacies*. Among Tachinidae, ecological niche appears to be a stronger determinant of host range than any phylogenetic relationship among host species (Crosskey, 1980). The only identified characteristic which is common to all the hosts of *T. brevifacies* recorded in New Zealand is that they are (at least facultative) concealed feeders as larvae. Host shelters of plant material and/or frass appear to function as a cue in host finding and oviposition by *T. brevifacies*. I have observed *T. brevifacies* females in the laboratory overlook stationary tortricid larvae not housed in leaf shelters preferring to investigate leaf shelters with tortricid larvae present or absent (Munro, unpub. data).

The forms of larval shelter used by the hosts of *T. brevifacies* are diverse. Tortricidae larvae and blackberry budmoth *E. phaulocosma* (Oecophoridae) join leaves or shoots with silk to form shelters (Nielsen and Common, 1991; Scott, 1984). Even occasional non-target hosts of *T. brevifacies* are concealed feeders. The native gelechiid *Stathmopoda skelloni* (Butler) feeds on dead and dying plant tissue and it has been known to utilise as shelters leaves that become curled as a result of apple leafcurling midge damage or colonise fruit calyces (Penman, 1984). Late instar larval stages of Pterophoridae feed on exposed leaf surfaces but they will also burrow into flower heads. Geometridae are usually

free living as larvae, however some species colonise new shoots or flowers of hebe resembling vegetal shelters, as is the case with *Pasiphila lunata* Philpott (Gaskin, 1966).

Feeding niche has been documented in other parasitoids as a factor that defines an otherwise phylogenetically distant group of hosts. For example, the ichneumonid *Endromopoda detrita*, parasitises a group of phytophagous insects that feed on grass stems including Diptera, Lepidoptera and small hymenopteran species (Godfray, 1994). Although polyphagy is widespread among Tachinidae (Askew and Shaw, 1986; Eggleton and Gaston, 1992; Belshaw, 1994), Australasian species of Tachinidae do not appear to have extreme host groups. However, within the tribe Blondeliini, to which *T. brevifacies* belongs, host ranges include several families, but exclusively within the orders Coleoptera, Lepidoptera or Hymenoptera (Crosskey, 1973).

Belshaw (1994) has analysed several tachinid life history characteristics and discussed their importance as mechanisms that facilitate reproduction on hosts with which they have not co-evolved. The three characteristics analysed were parasitoid reproductive strategy, the level of the parasitoids' development synchrony with a host, and location of parasitoid larva within the host. *Trigonospila brevifacies* oviposits macrotype eggs on late-instar hosts, and Belshaw (1994) showed that tachinid parasitoids employing this strategy do have significantly higher levels of polyphagy than the average for the Tachinidae. Belshaw (1994) hypothesized that koinobionts, (which are parasitoids whose hosts continue feeding for a period after parasitism (Godfray, 1994)), require greater physiological adaptation to hosts, because the juvenile parasitoid is exposed to a host's immune defenses for a longer period of time. Therefore, koinobionts should have narrower host ranges than idiobionts which kill or paralyse their hosts immediately. Although *T. brevifacies* fits the description of a koinobiont-like species, it can successfully reproduce on species from at least six lepidopteran families. This is assisted by partial encapsulation by the host, which forms a respiratory funnel around larval *T. brevifacies* when they invade a hosts body. The parasitoid larva maintains respiration through a hole in the host integument (Early, 1984). In a sense the parasitoid uses the host's defense system against it. The respiratory funnel allows the parasitoid to overcome the host's immune system defenses by preventing complete encapsulation and this enables it to parasitise a wide range of unrelated species (Askew and Shaw, 1986; Eggleton and Belshaw, 1993; Belshaw, 1994).

A summary of life history characteristics for *T. brevifacies* and whether they contribute to this parasitoids ability to reproduce on phylogenetically distant lepidopteran species is presented in Table 2.

Table 2. Life history characteristics of *Trigonospila brevifacies* and whether they contribute to this species ability to parasitise a wide range of host Lepidoptera (after Belshaw 1994).

Reproductive strategy	Oviposition onto host integument
Location of young larval parasitoid	Respiratory funnel
Development synchrony with host	Characteristics of koinobiont parasitoids
	- attacks late instar larvae
	- does not paralyse or kill host immediately
	* - therefore exposure to host's immune system defenses
	* - should require greater physiological adaptation to hosts

* respiratory funnels used by tachinid larvae help to overcome host immune defense system.

In conclusion, the availability of preferred hosts appears to determine when non-target hosts are attacked by *T. brevifacies*. The range of host species *T. brevifacies* parasitises appears to be delineated by host feeding niche behaviour.

Though the attack of non-target native Lepidoptera by *T. brevifacies* is an undesirable and predictable result, it is also an irreversible situation. The important outcome from this work is that archival host records, the study of parasitoid life history characteristics and host finding behaviour are useful and accurate predictors of *T. brevifacies* host range. Accurately focused field (in the region of origin), archival and laboratory testing of entomophagous biocontrol agents are required to predict host specificity. Therefore, broader criteria for testing host specificity, whereby environmental and biological cues are determined and used to define a list of potential non-target species, may prove more accurate predictors than simple choice / no-choice specificity testing.

REFERENCES

Askew, R.R., Shaw, M.R. (1986). Parasitoid communities: their size, structure and development. In: *Insect Parasitoids*. (J. Waage., P. Greathead., (Ed). Heinmann Educational Books Ltd, London, UK. pp 225-264.

Armstrong, K.F., Cameron, C.M., Frampton, E.R. and Suckling, D.M. (1997) Aliens at the border and cadavers in the field: a molecular technique for species identification. *Proceedings 50th New Zealand Plant Protection Conference*. pp 316-321.

Belshaw, R. (1994) Life history characteristics of Tachinidae (Diptera) and their effect on polyphagy. In: *Parasitoid community ecology* (B. A. Hawkins., W. Sheehan., Eds). Oxford University Press, Oxford, UK. pp 145-162.

Cameron, P.J., Hill, R.L., Bain, J., and Thomas, W.P. (1993) Analysis of importations for biological control of insect pests and weeds in New Zealand. *Biocontrol Science and Technology* **3**, 387-404

Cantrell, B.K. (1986) An updated host catalogue for the Australian Tachinidae (Diptera). *Journal of the Australian Entomological Society* **25**, 255-265.

Crosby, T. K., Dugdale, J. S., Watt, J. C. (1976) Recording specimen localities in New Zealand: an arbitrary system of areas and codes defined. *New Zealand Journal of Zoology* **3**, 69 plus map.

Crosskey, R.W. (1973) A conspectus of the Tachinidae (Diptera) of Australia, including keys of the supraspecific taxa and taxonomic and host catalogues. *The British Museum (Natural History) Entomology* Supplement **21**, 1-221.

Crosskey, R.W. (1980) Family Tachinidae. In: *Catalogue of the Diptera of the Afrotropical region*. (R.W. Crosskey., Ed). London. pp 822-882.

Cullen, J.M. (1997) Biological control and impacts on non-target species. *Proceedings of 50th New Zealand Plant Protection Conference*. pp 195-201.

Early, J.W . (1984) Parasites and predators. In: *New Zealand pest and beneficial insects* (R.R. Scott., Ed). Lincoln University College of Agriculture, Canterbury, New Zealand, pp 271-308.

Eggleton, P., Gaston, K.J. (1992) Tachinid host ranges: a reappraisal (Diptera: Tachinidae). *Entomologists Gazette* **43**, 139-143.

Eggleton, P., Belshaw, R. (1993) Comparisons of dipteran, hymenopteran and coleopteran parasitoids: provisional phylogenetic explanations. *Biological Journal of the Linnean Society* **48**, 213-226.

Freeman, D.H. (1987) Applied categorical data analysis. Marcel Dekker Inc, New York, USA.

Gaskin, D.E. (1966) The butterflies and common moths of New Zealand. Whitcombe and Tombs Ltd, Auckland, New Zealand.

Green, O. R. (1984) New Zealand host and locality records for an introduced tortricid parasite, *Trigonospila brevifacies* (Diptera: Tachinidae). *New Zealand Entomologist* **8**, 69-71.

Godfray, H.J.C. (1994) Parasitoids, behavioural and evolutionary ecology. Princeton University Press, New Jersey, USA.

Grenier, S. (1988) Applied biological control with tachinid flies (Diptera: Tachinidae): A review. *Anz. Schadlingskde., Pflanzenschutz, Umweltschutz* **61**, 49-56.

Gross, P. (1993) Insect behavioural and morphological defences against parasitoids. *Annual Review of Entomology* **38**, 251-273.

Hailemichael, Y., Smith, J.W., Wiedenmann, R.N. (1994) Host finding, host acceptance and host suitability of the parasite *Xanthopimpla stemmator*. *Entomologia Experimentalis et Applicata* **71,** 155-166.

Herrebout, W.M. (1969) Some aspects of host selection in *Eucarcelia rutilla* Vill. (Diptera: Tachinidae). *Netherlands Journal of Zoology* **19**, 1-104.

Janssen, A. (1989) Optimal host selection by *Drosophila* parasitoids in the field. *Functional Ecology* **3**, 469-479.

McCune, B. (1987) Multivariate analysis on the PC-ORD system. HRI report 75. Butler University.

Munro, V.M.W. (1997) *Eutorna phaulocosma* Meyrick (Lepidoptera: Oecophoridae), a new host for the introduced Australian parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae). *New Zealand Entomologist* **20**: 71-72.

Nielsen, E.S, and Common, I.F.B. (1991) Lepidoptera. In: *The insects of Australia, volume 2*. (I.F.B. Common., Ed) Melbourne University Press, Australia. pp 817-915.

Penman, D.R. (1984) Subtropical fruit pests. In: *New Zealand pest and beneficial insects*. (R.R. Scott., Ed). Lincoln University College of Agriculture, Christchurch, New Zealand. pp 51-64.

Roberts, L. I. N. (1986) The practice of biological control - implications for conservation, science and community. *The Weta* **9,** 76-84.

Russell, D.A. (1987) Parasitism of the oriental fruit moth *Grapholita molesta* (Lepidoptera: Tortricidae): The New Zealand position in the world perspective. *New Zealand Entomologist* **10**, 13-26.

Scott, R.R. (1984) Berry fruit pests. In: *New Zealand pest and beneficial insects*. (R.R. Scott., Ed). Lincoln University College of Agriculture, Christchurch, New Zealand. pp 11-32.

Singh, P. (1983) A general purpose laboratory diet mixture for rearing insects. *Insect Science and its Application* **4**, 357-362.

Strong, D.R., Lawton, J.H., Southwood, R. (1983) Insects on plants: community patterns and mechanisms. Blackwell Scientific Publications, London, UK.

Thomas, W.P. (1989) *Epiphyas postvittana*, the lightbrown apple moth. In: *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 187-195.

Wearing, C.H. (1994) National Leafroller Survey: Species Distribution Charts for Crops and Regions. *HortResearch Internal Report No. IR 94-64* pp 51.

Wilkinson, L., Blank, G., Gruber, C. (1996) Desk top data analysis with SYSTAT. Prentice Hall, New Jersey, USA.

Identification of shared parasitism between native lepidopteran parasitoid species and the biocontrol agent *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) in North Island forest habitats.

Abstract

The parasitoid guild attacking pre-imaginal Tortricidae on shrubs and small trees in broadleaf/podocarp forests was studied at six sites in the central North Island. Connectance and quantitative webs were used to interpret the complexities of host parasitoid interactions at a community level and identify competition between native parasitoids and the introduced species *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae). *Trigonospila brevifacies* is numerically dominant in the tortricid parasitoid guild. Its host range overlaps with 12 native and one introduced parasitoid species and it parasitises more species of Tortricidae than other parasitoids at the North Island forest sites surveyed. Quantification of the parasitoid load on native Lepidoptera indicated that *T. brevifacies* parasitism comprised between 15.6 % and 79.5 % of the parasitoid load per species. Only the introduced Australian canefruit pest *Eutorna phaulocosma* Meyrick (Lepidoptera: Oecophoridae) received a higher proportion of parasitism from *T. brevifacies* than any of the native Lepidoptera. The number of parasitoid species attacking each pre-imaginal host stage (except for pupae) of native Lepidoptera was relatively constant. The only pupal parasitoid recorded was the introduced ichneumonid *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae). All native parasitoid species were less abundant than *T. brevifacies*.

INTRODUCTION

Since the introduction of *T. brevifacies* to New Zealand in the late 1960s it has included in its host range non-target pest and non-pest lepidopteran species (Roberts, 1986; Green, 1984; Munro, 1997; Chapter 3). Although the parasitoid guild associated with pest Tortricidae of fruit crops in New Zealand has been extensively studied (Thomas, 1989; Wearing *et al*., 1991), no attempt has been made to identify native parasitoids with which *T. brevifacies* may be competing for hosts in forest habitats.

Tortricidae are the main hosts of *T. brevifacies* in native forests (Chapter 3). New Zealand Tortricidae have a high level of endemism. Of the 185 species of Tortricidae described, 174 are endemic to New Zealand. Six species have established in New Zealand

through human activities and one species is thought to have arrived by natural dispersal from Australia (Dugdale, 1988).

There are few experimental works quantifying the trophic links of parasitoid communities (Memmott *et al.*, 1994). Analysis of the structure of parasitoid-host guilds has been carried out in tropical leafminer communities (Memmott *et al.*, 1994); braconid parasitoids of aphids (Rejmanck & Stary, 1979); and ichneumonid parasitoids of leafminers from three insect orders (Shaw & Askew, 1976). The potential for parasitoid biological control agents to compete with native parasitoid fauna in new geographical ranges has mostly been overlooked by biocontrol practitioners. No previous attempt has been made in New Zealand to investigate the post-release, non-target effects of parasitoid biological control agents on native parasitoid fauna.

Parasitoids with overlapping host ranges may determine the diversity of host assemblages (Holt & Lawton, 1993). Parasitoid-host interactions at a community level can be interpreted using connectance and quantitative webs. Connectance webs are a useful method for identifying where competition is occurring between parasitoid species by graphing trophic links between parasitoids, herbivorous hosts and their host plants (Memmott *et al.*, 1994). They identify shared parasitism (i.e., where parasitoid host ranges overlap), apparent competition between hosts (i.e., where the abundance of one host species determines the abundance of parasitoids and where as a consequence, secondary host species of the parasitoid may receive higher rates of parasitism) and which key species dominate a community (Memmott *et al.*, 1994). Shared parasitism could result in competitive exclusion, which is defined as when interspecific competition between species (i.e., competition for hosts) results in the ecological separation of these species (Odum, 1983).

The aims of this work were: to use connectance webs to identify shared parasitism between *T. brevifacies* and native parasitoids attacking Lepidoptera in native forests; and to identify if these parasitoid species attack the same host life stages as *T. brevifacies*; to quantify parasitoid load for native Lepidoptera; and to identify whether *T. brevifacies* has become a dominant parasitoid species in the native forest communities it has invaded.

METHODS

Sites

Six North Island sites (three paired sites from three ecoregions) were surveyed to determine the range of species attacking larval and pupal stages of native Tortricidae in forest habitats. Paired sites were located at Rotoehu Forest (Bay of Plenty), Bushy Park and Pohangina Valley (Wanganui), and Tane and Mt. Bruce (Wairarapa). All forest sites were mature Broadleaf/Podocarp forests at altitudes of 200-300 m a.s.l., on level elevations (see Chapter 1 for further descriptions).

Sampling

Potential host larvae and pupae were collected during seven seasonal sampling occasions over a two-year period (1996-1998) at each site. The two host families attacked by *T. brevifacies* in New Zealand native forests are Tortricidae and Oecophoridae (Chapter 3). To ascertain which native parasitoid species *T. brevifacies* may be competing with for hosts in native forests, host sampling was limited to these two lepidopteran families. Forty Lepidoptera of larval and pupal stages were collected on each sampling occasion from each forest site. Hosts were collected at 2 m intervals along two 50 m transects, which were randomly placed on each sampling occasion, for a total of 84 transects. The time taken to collect 40 hosts provided an index of host density. Quantification of parasitoid density and the frequency of parasitism by parasitoids on host species collected was determined by rearing all Lepidoptera collected.

The host species were identified and approximate ages (by instar-size) of host specimens were determined in the laboratory soon after collection (using J.S. Dugdale, unpub. data). Host plants were identified by referring to Salmon (1980) or herbarium records held at Massey University. Larvae were transferred to vials of artificial diet (Singh, 1983) and allowed to develop in the laboratory at 18 ± 2 °C and LD:16/8. Pupating Tortricidae or parasitoids were monitored daily until emergence of either an adult moth or a parasitoid. Parasitoids were identified by a specialist taxonomist (J. Berry, Landcare Research).

Host samples provided data on the structure of the tortricid guild and relative abundance of host species, parasitoid load for each host species and the host lifestage attacked by each parasitoid species collected.

Data analysis

In the present study an aim was to determine the native parasitoid species with which *T. brevifacies* shared hosts. To maintain consistency in the analysis, two pairs of closely related species were combined in the quantitative analysis. First, the abundance and parasitism of the hosts *Planotortrix excessana* (Walker) and *Planotortrix octo* (Walker) (Tortricidae) were combined as they can not be reliably differentiated as larvae and no molecular genetic test is available to determine between these species. Second, the native parasitoids *Pales feredayi* (Hutton) and *Pales funesta* (Hutton) (Diptera: Tachinidae) were not separated to species on all occasions of the present study. A connectance web was constructed to illustrate the relationships between plant species, tortricid hosts and parasitoids found at the six North Island, native forest sites. Secondly, a quantitative web was constructed where the relative densities of hosts and parasitoids were presented to illustrate the abundance of hosts and their relative parasitoid loads.

RESULTS

Community description

Lepidoptera were collected from 37 plant species from 28 families at the six North Island forest sites. The 15 species of Tortricidae and Oecophoridae collected were parasitised by 14 parasitoid and one nematode parasite species. All 13 species of Tortricidae collected belonged to the subfamily Tortricinae and Tribe Archipini, with the exception of *Strepsicrates ejectana* (Walker) which is in the subfamily Olethreutinae. The two oecophorid species belonged to different subfamilies. The native species *Hierodoris atychioides* (Butler) is in Oecophorinae and the Australian cane fruit pest *Eutorna phaulocosma* Meyrick belongs to the subfamily Depressariinae. Most Lepidoptera sampled were polyphagous, feeding on more than 6 host plants, and *Ctenopseustis obliquana* (Walker) (Lepidoptera: Tortricidae) was collected from a total of 31 plant species. Three species were collected from only one plant. In two cases, *Leucoteus coprosmae* Dugdale and *Apoctena orthropis* (Meyrick), this may be attributed to the rarity of the lepidopterans rather than host specificity *per se*. The other case the introduced species *E. phaulocosma*, was found to feed only on the introduced blackberry *Rubus fruticosus* L. agg., although another Rosaceae species, the native lawyer vine *Rubus cissoides,* occurred at most sites.

The parasitoid guild consisted of 11 hymenopteran parasitoids, belonging to the families Braconidae, Ichneumonidae and Eulophidae, and three species of Tachinidae

(Diptera). Most parasitoids were collected from more than one host. Eight of the parasitoid species attacked between 2 and 4 host species. *Trigonospila brevifacies* parasitised the biggest range of Lepidoptera, attacking seven host species (eight species in total if *P. excessana* and *P. octo* were treated separately). Three parasitoid species, *Dolichogenidea* sp.3 (Braconidae), *Dolichogenidea tasmanica* (Cameron) (Braconidae), and *Euceros coxalis* Barron (Ichneumonidae), were recorded from a single host species. The apparent host specificity of these parasitoids may be attributable to the small number of individuals of these species collected, as at least *D. tasmanica* is known to parasitise more than one tortricid species (Early, 1984). One species of parasite, the nematode *Hexameris albicans* (von Siebold) (Mermithidae), was only ever reared from the native brownheaded leafroller *Ctenopseustis obliquana* (Walker) (Tortricidae). A connectance web summarises the interactions between the host plants fed upon by host Lepidoptera and the shared parasitism of host species by *T. brevifacies* and native parasitoids (Figure 1 & Table 1).

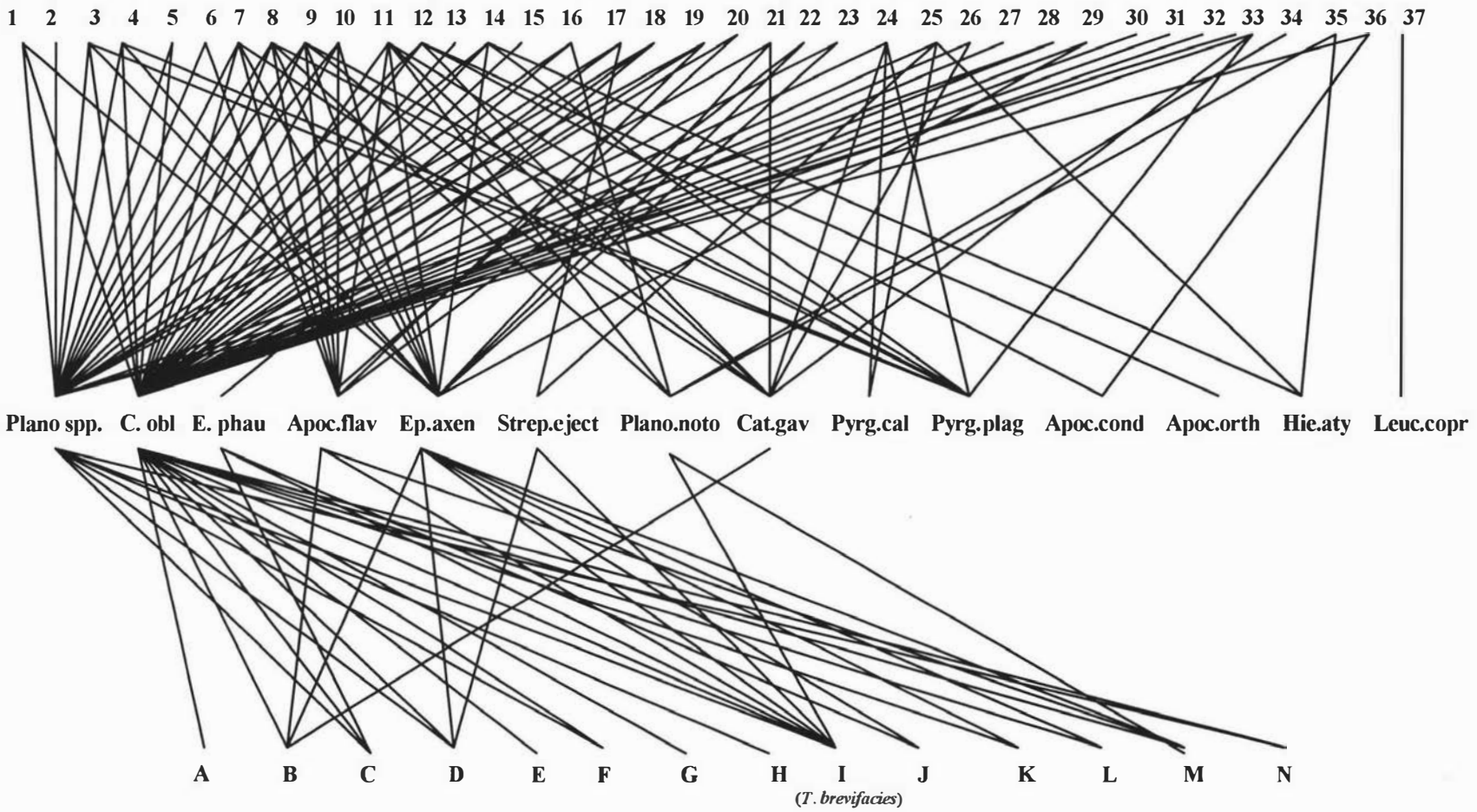


Figure 1. Trophic connectance web of host plants, Lepidoptera and their parasitoids at six native forests sites. Level 1: host plants of Lepidoptera; Level 2: host Tortricidae and Oecophoridae; Level 3: parasite and parasitoid species attacking Lepidoptera. See Table 1 for species codes.

Table 1. Names of plant, lepidopteran and parasitoid species relating to codes in figure 1.

Plant species

1 fuchsia *Fuchsia exorticata* (F: Onagraceae)
2 fern *Cyclosorus penniger*
3 mapau *Myrsine australis* (F: Myrsinaceae)
4 pukatea *Laurelia novae-zelandiae* (F: Monimiaceae)
5 rangiora *Brachyglottis repanda* (F: Compositae)
6 ribbonwood *Plagianthus regius* (F: Malvaceae)
7 pigeonwood *Hedycarya arborea* (F: Monimiaceae)
8 wineberry *Aristotelia serrata* (F: Elaeocarpaceae)
9 willow *Salix alba* (F: Salicaceae)
10 kawakawa *Macropiper excelsum* (F: Piperaceae)
11 mahoe *Melicytus ramiflorus* (F: Violaceae)
12 tawa *Beilschmiedia tawa* (F: Lauraceae)
13 rata *Metrsideros umbellata* (F: Myrtaceae)
14 titoki *Alectryon excelsus* (F: Sapindaceae)
15 bush lawyer vine Rubus cissoides (F: Rosaceae)
16 kanono *Coprosoma grandifolia* (F: Rubiaceae)
17 miro *Prumnopitys ferruginea* (F: Podocarpaceae)
18 blackberry *Rubus fruticosus* (F: Rosaceae)
19 parconsia vine *Parsonsia heterophylla* (F: Apocynaceae)
20 putaputaweta *Carpodetus serratus* (F: Escalloniaceae)
21 pate *Schefflera digitata* (F: Araliaceae)
22 hangehange *Geniostoma rupestre* (F: Loganiaceae)
23 rewarewa *Knightia excelsa* (F: Proteaceae)
24 kaikomiko *Pennantia corymbosa* (F: Icacinaceae)
25 manuka *Leptospermum scoparium* (F: Myrtaceae)
26 karamu *Coprosoma robusta* (F: Rubiaceae)
27 maire *Nestegis cunninghamii* (F: Oleaceae)
28 lemonwood *Pittosporum eugenioides* (F: Pittosporaceae)
29 buddleia *Buddleia davidii* (F: Buddlejaceae)
30 rata vine *Metrosideros umbellata* (F: Myrtaceae)
31 kahikatea *Dacrycarpus dacrydioides* (F: Podocarpaceae)
32 ramarama *Lophomyrtus bullata* (F: Myrtaceae)
33 hutu *Ascarina lucida* (F: Chloranthaceae)
34 pine *Pinus radiata* (F: Pinaceae)
35 matai *Prumnopitys taxifolia* (F: Prumnopitys)
36 supplejack vine *Ripogonum scandens* (F: Liliaceae)
37 *Coprosoma rotundafolia* (F: Rubiaceae)

Host species

Plano spp. = *Planotortrix octo & P. excessana* (F: Tortricidae)
C.obl = *Ctneopseustis obliquana* (F: Tortricidae)
E.phau = *Eutorna phaulocosma* (F: Oecophoridae)
Apoc.flav = *Apoctena flavescens* (F: Tortricidae)
Ep.axen = *Epalxiphora axenana* (F: Tortricidae)
Strep.eject = *Strepsicrates ejectana* (F: Tortricidae)
Plano.noto = *Planotortrix notophaea* (F: Tortricidae)
Cat.gav = *Catamacta gavisana* (F: Tortricidae)
Pyrg.cal = *Pyrgotis calligypsa* (F: Tortricidae)
Pyrg.plag = *Pyrgotis plagiatana* (F: Tortricidae)
Apoc.cond = *Apoctena conditana* (F: Tortricidae)
Apoc.orth = *Apoctena orthropis* (F: Tortricidae)
Hie.aty = *Hierodoris atychioides* (F: Oecophoridae)
Leuc.copr = *Leucoteus coprosomae* (F: Tortricidae)

Parasitoid and parasite species

A *Diadegma* sp. (F: Braconodae)
B *Meteorus cinctellus* (F: Braconidae)
C *Dolichogenidea carposinae* (F: Braconidae)
D *Dolichogenidea* sp. 1 (F: Braconidae)
E *Dolichogenidea* sp. 3 (F: Braconidae)
F *Zealachertus* sp. 5 (F: Chalcidoidea)
G *Dolichogenidea tasmanica* (F: Braconidae)
H *Euceros coxalis* (F: Ichneumonidae)
I *Trigonospila brevifacies* (F: Tachinidae)
J *Pales feredayi* and *Pales funesta* (F: Tachinidae)
K *Carria fortipes* (F: Ichneumonidae)
L *Sympiesis* sp. (F: Chalcidoidea)
M *Campoplex* sp. (F: Ichneumonidae)
N *Hexameris albicans* (F: Mermithidae)

The different pre-imaginal larval stages of Lepidoptera were parasitised by similar numbers of parasitoid species (Table 2). Early-instar hosts were parasitised by eight species mostly from the family Braconidae. Mid-instar hosts were attacked by nine species predominately from the families Braconidae and Ichneumonidae. The eight species parasitising late-instar larvae were mainly Tachinidae and Ichneumonidae. The nematode species, *H. albicans*, is specific to *C. obliquana* (Woutts, 1984) and attacked mid and late instar larvae of this species. The pupae of hosts were poorly represented in samples. The introduced Australian biocontrol agent, *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae) is a known parasitoid of tortricid pupae and it has been recorded parasitising native Tortricidae on a few occasions in native forests (NZNAC, unpub. records), but none were recorded in the present study. Over a three year period, *X. rhopaloceros* was seen in gardens near forest areas, but never in the forest proper.

Table 2. Parasitoids and parasites of tortricid and oecophorid species within *Trigonospila brevifacies* host range occurring in North Island forests.

Host stage collected	Parasitoid/Parasite Species	Family
Early instars	*Diadegma* sp.	Braconidae: Microgastrinae
	Meteorus cinctellus (Spinola)	Braconidae: Euphorinae
	Dolichogenidea carposinae	Braconidae: Microgastrinae
	Dolichogenidea sp. 1	Braconidae: Microgastrinae
	Dolichogenidea sp. 3	Braconidae: Microgastrinae
	Zealachertus sp. 5	Eulophidae
	Dolichogenidea tasmanica (Cameron)	Braconidae: Microgastrinae
	Euceros coxalis Barron	Ichneumonidae: Eucerotinae
Mid-instars	*Pales feredayi* (Hutton)	Tachinidae
	Carria fortipes Cameron	Ichneumonidae: Metopiinae
	Sympiesis sp.	Eulophidae
	Meteorus cinctellus (Spinola)	Braconidae: Euphorinae
	Campoplex sp.	Ichneumonidae: Campopleginae
	Dolichogenidea sp. 1	Braconidae: Microgastrinae
	Diadegma sp.	Braconidae: Microgastrinae
	undescribed sp.	Ichneumonidae: Ichneumoninae
	Hexameris albicans	Nematode: Mermithidae
Late instars	*Meteorus cinctellus* (Spinola)	Braconidae: Euphorinae
	Sympiesis sp.	Eulophidae
	Pales feredayi (Hutton)	Tachinidae
	Pales funesta (Hutton)	Tachinidae
	Campoplex sp.	Ichneumonidae: Campopleginae
	Carria fortipes Cameron	Ichneumonidae: Metopiinae
	Hexameris albicans	Nematode: Mermithidae
	Trigonospila brevifacies (Hardy)	Tachinidae: Blondeliini
Pupae	*Xanthopimpla rhopaloceros* Krieger	Ichneumonidae: Pimplinae

Parasitoid load

The mean number of parasitoid species (collected during the two year field survey) attacking each leafroller species was 4.75. *Ctenopseustis obliquana* was parasitised by 12 species of parasitoid. In the present study *E. phaulocosma* was parasitised by the Australian tachinid *T. brevifacies*, the native tachinid *P. funesta* and the native braconid *Dolichogenidea carposinae* Wilkinson. Both *D. carposinae* and *T. brevifacies* parasitised the larval stages of *E. phaulocosma,* the former attacking early-instar larvae and the latter late-instar larvae. While *P. funesta* oviposits on vegetation near host larvae which then ingest the tachinids eggs (Early, 1984). Though only one *P. funesta* individual develops per host, in the present study both *T. brevifacies* and *P. funesta* were found to be able to develop within a single host, possibly because they develop in different parts of the host.

Trigonospila brevifacies constituted between 15.6 % and 80 % of parasitism occurring on host Lepidoptera sampled. *Trigonospila brevifacies* was the dominant parasitoid species of all host species except *Epalxiphora axenana* Meyrick and *S. ejectana* (Figure 2). The three tachinid species made up 51 % of all parasitism that occurred (Figure 3). *Trigonospila brevifacies* attacked the most species of host and had the highest level of parasitism across the host guild (Figure 4a & 4b). When abundance of each host species was expressed as a percentage of the total number of hosts collected during the surveys, *C. obliquana* was the most abundant species followed by the two *Planotortrix* species and *E. axenana* (Figure 5a). The overall rate of parasitism across host species ranged from 13 % to 26.5 % of each host species population. The least abundant host species, *S. ejectana* had the highest percentage (26.5 %) of individuals parasitised in samples and the most abundant host, *C. obliquana,* received the fourth highest level of parasitism (20.79 %) (Figure 5b).

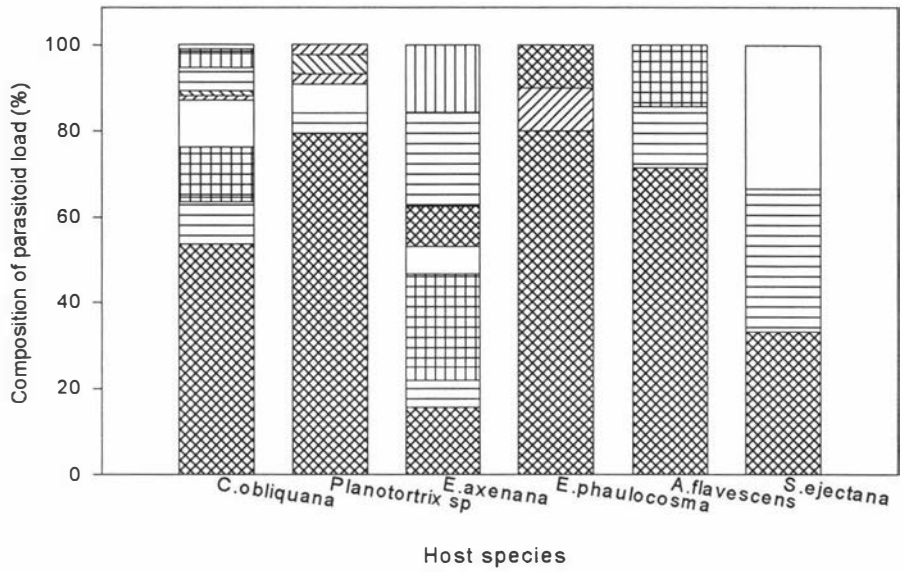


Figure 2. Comparison of the contribution of *T. brevifacies* to the parasitoid load of six non-target lepidopteran species. Parasitoid species are represented as follows:

Trigonospila brevifacies
Campoplex sp.
Diadegma sp.
Meteorus cinctellus
Dolichogenidea sp.1
Dolichogenidea carposinae
Zealachertus sp. 5
Pales spp.
Carria fortipes
Sympiesis sp.
Dolichogenidea sp.3
Dolichogenidea tasmanica
Euceros coxalis

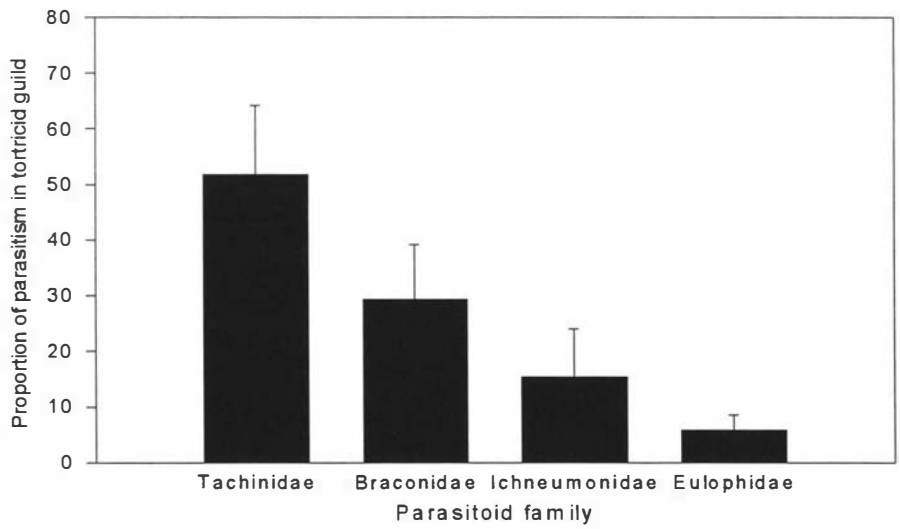


Figure 3. Proportion of tortricid host mortality contributed by the four parasitoid families. Error bars represent standard error.

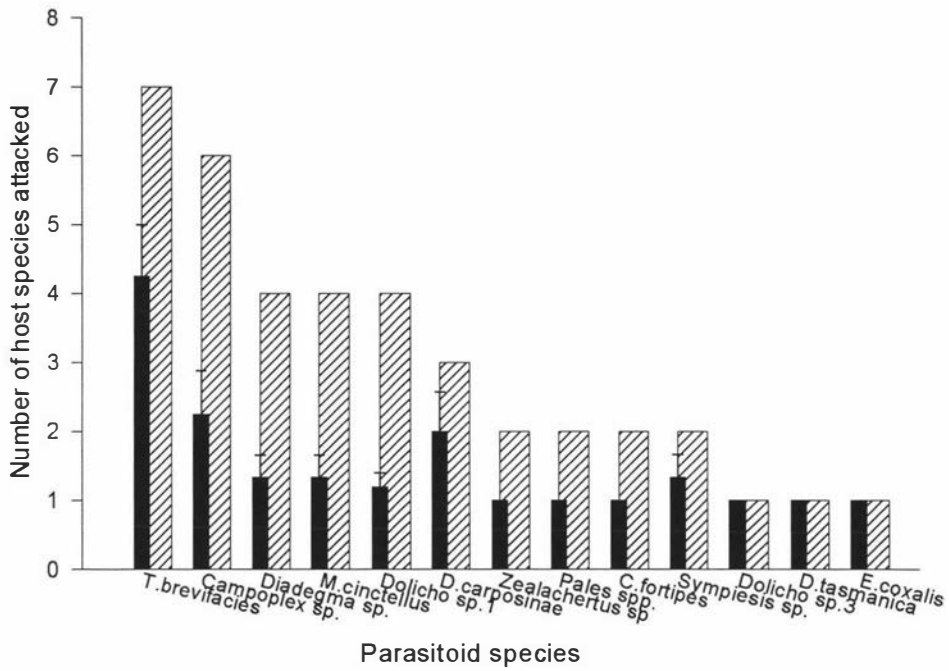


Figure 4a. The total number of lepidopteran species parasitised by each parasitoid species (hatched bars). The mean number of hosts parasitised by each parasitoid across the six study sites (solid bars). Error bars represent standard errors.

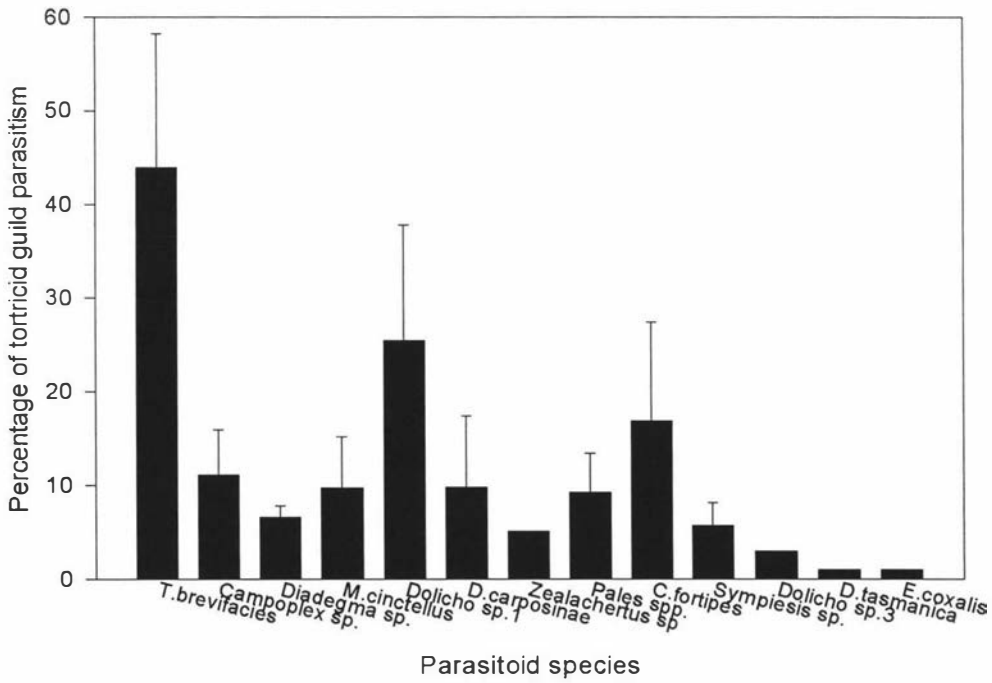


Figure 4b. Comparison of the levels of parasitism by *T. brevifacies* and other parasitoid species attacking non-target lepidopteran species. Error bars represent standard errors.

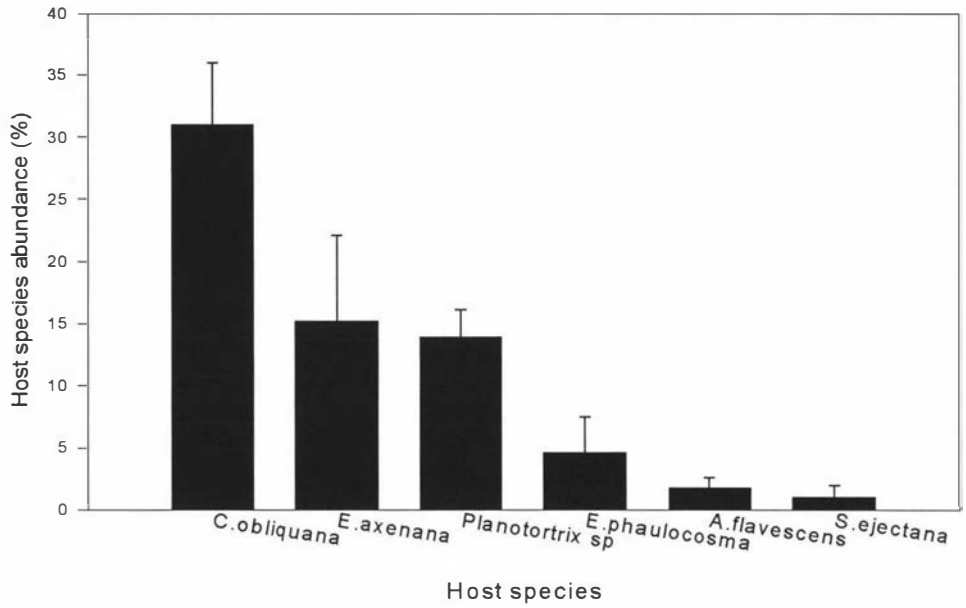


Figure 5a. Relative abundance of the seven most common lepidopteran taxa parasitised by *T. brevifacies* (*P.octo* and *P. excessana* are combined as *Planotortrix* spp.). Error bars represent standard errors.

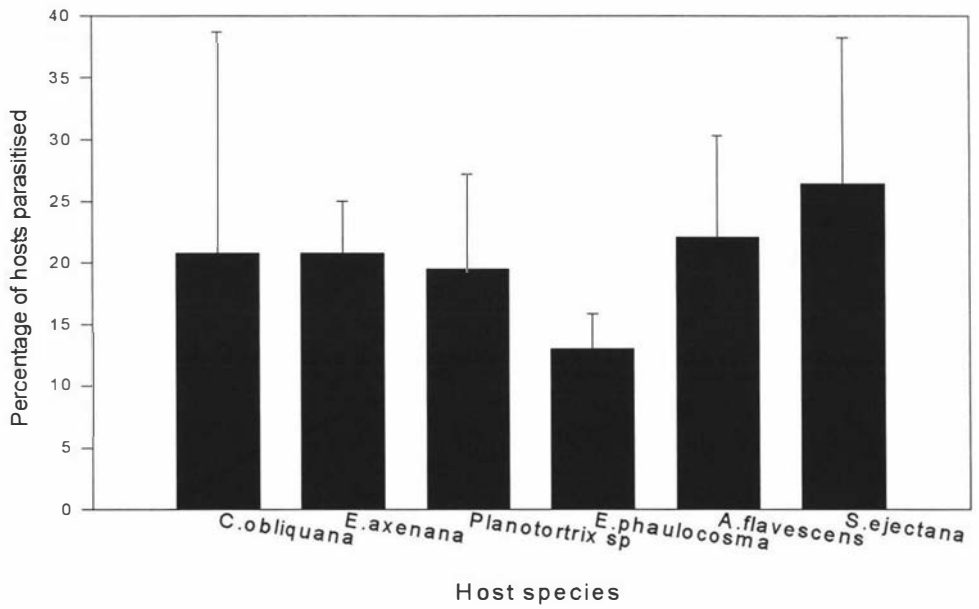


Figure 5b. The combined percentage parasitism by *T. brevifacies* and 12 other parasitoid species on seven lepidopteran taxa (*P.octo* and *P. excessana* are combined as *Planotortrix* spp.). Error bars represent standard errors.

Quantitative web of parasitoid host overlap

Five tortricids and one species of oecophorid included in the connectance web were removed for the quantitative analysis as no parasitoids were recorded for these Lepidoptera, leaving eight lepidopteran and 14 parasitoid species (13 when the two *Pales* species are combined as *Pales* spp.) (Figure 6). Although this is relatively small number of host and parasitoid species, 37 types of interaction (i.e., parasitoid/host) were recorded.

Specific patterns of interaction between parasitoids and their hosts become apparent in the quantitative web. The quantitative web indicates that the host range of *T. brevifacies* overlaps with part or all of the host range of the 13 other parasitoid species. All other parasitoids recorded were less abundant than *T. brevifacies*. The rarest parasitoids, *D. carposinae*, *Dolichogenidea* sp.3, *Zealachertus* sp.5, *D. tasmanica* and *Euceros coxalis*, were recorded from the most abundant hosts, the combined *Planotortrix* species and *C. obliquana*. The ichneumonid, *Carria fortipes* Cameron, was the only species among the abundant parasitoid group which spread its parasitism equitably among its two hosts, with *C. obliquana* receiving 46 % and *E. axenana* 55 % of the total parasitism.

The majority of common parasitoid species parasitising more than two hosts obtained between 43 % and 64 % of their hosts from one lepidopteran species. *Ctenopseustis obliquana*, the *Planotortrix* species and *E. axenana* were the most abundant host species in this guild. *Ctenopseustis obliquana* and *E. axenana* were the primary hosts of the most abundant parasitoid species and in most cases the secondary hosts in each parasitoids' host range were less common in the forests surveyed.

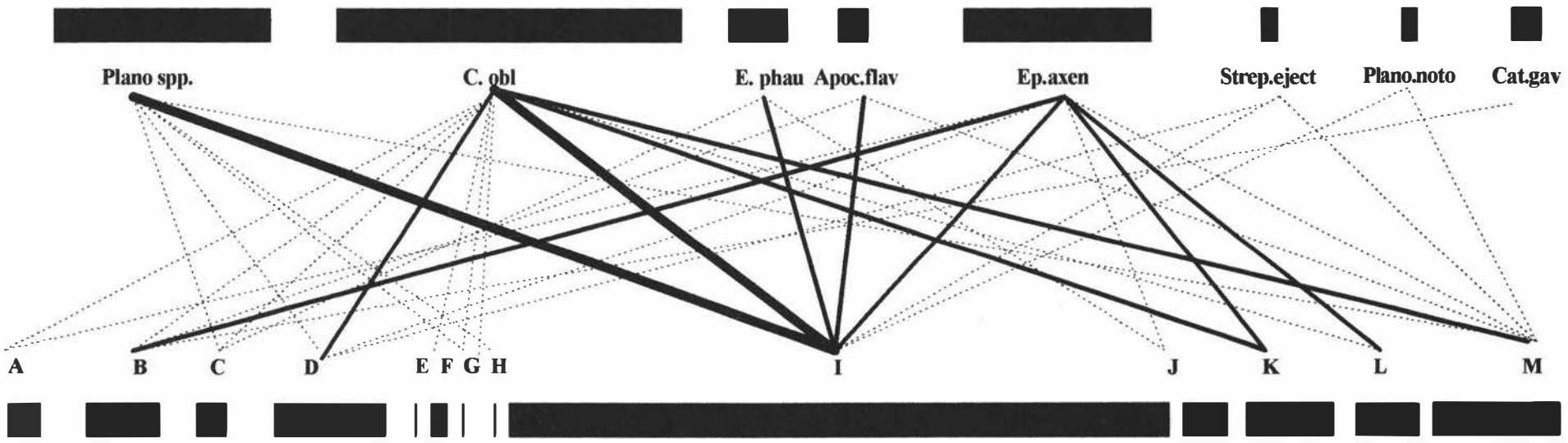


Figure 6. Quantitative web illustrating the relative abundance of species within the parasitoid complex and Lepidoptera parasitised by *Trigonospila brevifacies* and other parasitoids in native forests. Level 1: host Lepidoptera; Level 2: parasitoid species overlap. Relative abundance of host species in each parasitoids diet represented by line thickness, 1-3 parasitoids reared ····· 4-15 parasitoids reared ——— >16 parasitoids reared ▬▬ (data next page).

Scale: ▬ = 10 parasitoids ▬ = 100 hosts

Host species

Plano spp. = *Planotortrix octo* & *P. excessana* (Tortricidae)
C.obl = *Ctneopseustis obliquana* (Tortricidae)
E.phau = *Eutorna phaulocosma* (Oecophoridae)
Apoc.flav = *Apoctena flavescens* (Tortricidae)
Ep.axen = *Epalxiphora axenana* (Tortricidae)
Strep.eject = *Strepsicrates ejectana* (Tortricidae)
Plano.noto = *Planotortrix notophaea* (Tortricidae)
Cat.gav = *Catamacta gavisana* (Tortricidae)

Parasitoid species

A *Diadegma* sp. (F: Braconodae)
B *Meteorus cinctellus* (F: Braconidae)
C *Dolichogenidea carposinae* (F: Braconidae)
D *Dolichogenidea* sp. 1 (F: Braconidae)
E *Dolichogenidea* sp. 3 (F: Braconidae)
F *Zealachertus* sp. 5 (F: Chalcidoidea)
G *Dolichogenidea tasmanica* (F: Braconidae)
H *Euceros coxalis* (F: Ichneumonidae)
I *Trigonospila brevifacies* (F: Tachinidae)
J *Pales feredayi* and *Pales funesta* (F: Tachinidae)
K *Carria fortipes* (F: Ichneumonidae)
L *Sympiesis* sp. (F: Chalcidoidea)
M *Campoplex* sp. (F: Ichneumonidae)

Parasitoid species	Host species	Number of interactions
Diadegma sp.	*Ctenopseustis obliquana*	2
	Epalxiphora axenana	2
Meteorus cinctellus	*Ctenopseustis obliquana*	2
	Epalxiphora axenana	7
	Apoctena flavescens	1
	Catamacta gavisana	1
Dolichogenidea carposinae	*Planotortrix spp.*	1
	Ctenopseustis obliquana	1
	Eutorna phaulocosma	1
Dolichogenidea sp.1	*Planotortrix spp.*	3
	Ctenopseustis obliquana	10
	Epalxiphora axenana	2
	Strepsicrates ejectana	1
Dolichogenidea sp.3	*Ctenopseustis obliquana*	1
Zealachertus sp.5	*Planotortrix spp.*	1
	Ctenopseustis obliquana	1
Dolichogenidea tasmanica	*Ctenopseustis obliquana*	1
Euceros coxalis	*Planotortrix spp.*	1
Trigonospila brevifacies	*Planotortrix spp.*	37
	Ctenopseustis obliquana	49
	Eutorna phaulocosma	8
	Apoctena flavescens	5
	Epalxiphora axenana	5
	Strepsicrates ejectana	1
	Planotortrix notophaea	1
Pales spp.	*Eutorna phaulocosma*	3
	Epalxiphora axenana	1
Carria fortipes	*Ctenopseustis obliquana*	6
	Epalxiphora axenana	5
Sympiesis sp.	*Ctenopseustis obliquana*	3
	Epalxiphora axenana	5
Campoplex sp.	*Planotortrix spp.*	2
	Ctenopseustis obliquana	9
	Apoctena flavescens	1
	Epalxiphora axenana	2
	Strepsicrates ejectana	1
	Planotortrix notophaea	3

DISCUSSION

Consideration of non-target effects by biocontrol agents on native parasitoids

This is the first work in New Zealand that attempts to determine the impact of a parasitoid, introduced as a biological control agent, on the native parasitoid fauna. The impact that biological control agents may have on native insect natural enemies when introduced to new geographical areas is not usually considered when testing the suitability of a candidate parasitoid species for release. The rationale is that if parasitoid biological control agents are considered for introduction, it is because existing biological control is insufficient to control the target pest species and therefore an introduced parasitoid would be less likely to come into competition with other parasitoids.

Several assumptions support the argument that parasitoid biological control agents and native parasitoids are unlikely to overlap. Target pest species are often from another geographical location, (although some polyphagous native species become pests of exotic crops) and if the pest species is not closely related to native hosts in the new location few native parasitoids would be physiologically adapted to overcome the immune defenses of pest species. Even when native natural enemy and introduced biocontrol agents attack the same host species habitat preferences may separate the parasitoid species. For example, biocontrol agents attacking pest species occurring in pastoral or horticultural environments are less likely to compete for hosts with native parasitoids. Presently, parasitoid species chosen for release are host specific or confined to a narrow host guild of closely related species and almost always the target host is an exotic species.

The generalist parasitoid *T. brevifacies* has invaded native forests and now directly competes with the parasitoid assemblage associated with the eight non-target lepidopteran species it attacks (Chapter, 3; Chapter 7). This situation is not unique in New Zealand. The parasitoid *Microctonus aethiopoides* Loan (Braconidae), introduced to control the weevil *Sitona discoideus* Gyllenhal has been reared from eight species of native non-target weevil in the field (Barratt, *et al.*, 1996). When both *M. aethiopoides* and *T. brevifacies* were introduced, host specificity was not as strict a requirement as it is at present. Also, polyphagy was regarded as a desirable trait for a candidate biocontrol agent because polyphagous species were considered more likely to establish (Cameron *et al.*, 1993). As yet no work has been carried out to quantify the impact of *M. aethiopoides* on the native parasitoids associated with the non-target native Curculionidae attacked by this biological control agent. Another example concerns the parasitoid *Diglyphus iseae* Walker

(Hymenoptera: Eulophidae) which was introduced to New Zealand in 1969 to control the chrysanthemum leaf miner *Chromatomyia syngenesiae* (Hardy) (= *Phytomyza aticornis*) (Diptera: Agromyzidae) (Cameron *et al.*, 1989). The parasitoid has since invaded native subalpine habitats in the South Island of New Zealand and has been recorded parasitising a non-target native leaf miner, *Liriomyza* sp. (Diptera: Agromyzidae) on hebe (H.C.J. Godfray, pers. comm., 1997).

Non-target effects of *Trigonospila brevifacies* on native parasitoids

When *T. brevifacies* was introduced to New Zealand the possible impact of the tachinid on native parasitoids was discussed, but less importance was attached to this prospect than would be the case today (C.H. Wearing, pers.comm. 1999). One of the non-target impacts of *T. brevifacies* not foreseen was the potential for it to compete directly (or indirectly) with native parasitoids by invading forest habitats. *Trigonospila brevifacies* is now known to share its host range with 13 native parasitoid species and all these parasitoid species were less abundant than *T. brevifacies* in the forest habitats surveyed. Sampling effort in a broader range of North Island forest types, altitudes and climatic conditions is needed to determine the full extent of host sharing between *T. brevifacies* and native parasitoid species.

With host range overlap confirmed between *T. brevifacies* and native parasitoids, competitive exclusion of native species is an undesired impact that may occur. Host specific parasitoid species are most likely to be affected by competition from *T. brevifacies* where the host species is rare and parasitism by *T. brevifacies* on this host is significant. Conversely, if a rare host specific parasitoid is competing with *T. brevifacies* for an abundant host species, the impact of this competition is less likely to result in competitive exclusion. Three rare host specific native parasitoid species were found to parasitise the three most abundant tortricid species *C. obliquana* and *P. octo* and *P. excessana.* No instances of host specific parasitoids parasitising rare hosts were detected in the quantitative web. This may be because there are no host specific parasitoids of these rare host species; they may have already been displaced by *T. brevifacies*; or they may not have been detected because their hosts were under represented by the sampling procedure. For example, the primary host of the parasitoid *D. carposinae,* which was rare in this study, is thought to be the native carposinid moth *Heterocrossa adreptella* Walker (J. Charles, pers. comm.). *Heterocrossa adreptella* was not detected in the present study, probably because canes were not sampled and the larvae of this species burrow into soft cane. But a few *D.*

carposinae emerged from samples of *C. obliquana*, *Planotortrix* spp. and *E. phaulocosma* hosts. So a parasitoid that appears to be rare on the quantitative web and may be competing with *T. brevifacies* for hosts, actually has a primary host that *T. brevifacies* is not known to attack and is unlikely to parasitise given the feeding niche the host occupies (Chapter 3). Therefore the level of competition for hosts between these two parasitoids is likely to be less than anticipated. Study of communities in which *T. brevifacies* has not yet established or experimental manipulations are required to demonstrate whether *T. brevifacies* is likely to displace native parasitoids.

Shared host range is not the only factor to influence the degree of competition between species and ultimately the structure of a parasitoid guild. The host life stage parasitised could determine the impact of *T. brevifacies* competition on native parasitoids. Models assessing the effect of life stage on interspecific parasitoid competition predict that parasitoids attacking earlier life stages have a competitive advantage over those attacking later life stages (Briggs, 1993). Most examples of competitive displacement among parasitoids come from the sphere of biological control (Godfray, 1994) and involve a single host species. Retrospective assessment of the parasitoid complex associated with the Californian red scale, *Aonidiella aurantii* (Maskell) (Hemiptera), indicates that *Aphytis lingnanenis* Compere (Hymenoptera: Aphelinidae) was competitively excluded by the later introduction of *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) which attacks an earlier host stage (Murdoch *et al.*, 1996). *Trigonospila brevifacies* parasitises late-instar larvae while eight of the native parasitoids and the self-introduced species *D. tasmanica* were found to parasitise early and mid-instar hosts. Therefore, it is possible that the impact of *T. brevifacies* on native parasitoids of earlier host life stages may be minor. A factor which may have minimised the effect of established parasitoids on the invading *T. brevifacies* is that *T. brevifacies* is a polyphagous species, as are many of the parasitoids it competes with for hosts. Anecdotal reports suggest that the introduced tortricid biological control agent *X. rhopaloceros* was abundant in the North Island during the 1970s (MAF, 1975; MAF, 1976; Mckenzie 1981), but later observations indicate a decline in abundance (J.Walker pers.comm., 1997). The absence of the pupal parasitoid *X. rhopaloceros* from forest samples may suggest competitive exclusion by *T. brevifacies,* a parasitoid of earlier larval life stages.

A host species abundance can determine the abundance of it's primary parasitoid and indirectly the abundance of other parasitoid species by a mechanism called apparent competition. Apparent competition usually refers to cases where an abundant primary host species affects the level of parasitism exerted by a shared parasitoid on a less abundant secondary host. However, the abundance of any other parasitoids of the secondary host, especially host specific parasitoids, may also be affected. Only one well documented example is believed to successfully demonstrate apparent competition (Godfray, 1994). Two grape leafhoppers of the same genus, the endemic *Erythroneura elegantula* and the invader species *Erythroneura variabilis* (Hemiptera), are parasitised by *Anagrus epos* (Hymenoptera: Mymaridae). When *E. variabilis* invaded a region occupied by *E. elegantula* and became abundant, the parasitoid *A. epos* also increased in number and subsequently affected the abundance of the secondary host *E. elegantula*. The location of *E. elegantula* eggs on leaves makes it more susceptible to *A. epos* and as a consequence *E. elegantula* declined in number (Settle & Wilson, 1990). However, no mention is made of any secondary parasitoids of *E. elegantula* that may have been affected by it's decline. In the system that *T. brevifacies* has invaded any patterns that may suggest apparent competition should be considered with caution as no data exists regarding the relative abundance of the lepidopteran species prior to *T. brevifacies* release.

Several mechanisms could minimise the impact that host species can have on one another through apparent competition and so the indirect effects their associated parasitoids have on each another. These include; donor-controlled systems, where polyphagous parasitoids that do not respond in a density dependent manner, do not regulate host abundance. The resource limitation of dominant hosts, where the dominant host species abundance is limited by resource competition and therefore the impact of the parasitoid on the secondary host is lessened. Spatial refuges, where a number of hosts escape parasitism by utilizing enemy free space. Temporal refuges, where a proportion of a host species is asynchronous with a parasitoids lifecycle and so avoids parasitism. Regional co-existence, where different host species are dominant at various locations within a region and so when assessed as a whole several competing species are observed to co-exist (Holt & Lawton, 1993). Data from the present study indicate that the centre of forests provide refuges for host Lepidoptera from *T. brevifacies* parasitism (Chapters 6 & 7). As a consequence of this enemy free space, the impact of *T. brevifacies* on secondary hosts and therefore any host specific parasitoids may be lessened.

In conclusion, data from the present study indicates that *T. brevifacies* is competing with several native parasitoids for host Lepidoptera and has become the dominant parasitoid species in the leafroller guild. *Trigonospila brevifacies* may be having undesirable effects on native fauna by displacing native parasitoids through direct competition and affecting the population size of less abundant native Lepidoptera and indirectly any host specific parasitoids through apparent competition. Empirical studies of a simplified controlled host-parasitoid community, and of the structure of host-parasitoid communities before and after the release of *T. brevifacies* would be required to determine if native parasitoid displacement were actually occurring.

REFERENCES

Barratt, B.I.P., Evans, A.A., Johnstone, P.D. (1996) Effect of the ratios of *Listronotus bonariensis* and *Sitona discoideus* (Coleoptera: Curculionidae) to their respective parasitoids *Microctonus hyperodae* and *Microctonus aethiopoides* (Hymenoptera: Braconidae), on parasitism, host oviposition and feeding in the laboratory. *Bulletin of Entomological Research* **86**: 101-108.

Briggs, C.J. (1993) Competition among parasitoids on a stage-structured host and its effect on host suppression. *American Naturalist* **141**: 372-397.

Cameron, P.J., Hill, R.L., Bain, J., and Thomas, W.P. (1993) Analysis of importations for biological control of insect pests and weeds in New Zealand. *Biocontrol Science and Technology* **3**, 387-404.

Dugdale, J.S. (1988) Lepidoptera - annotated catalogue, and keys to family-group taxa. DSIR Science Information Publishing Centre, Wellington, New Zealand.

Early, J.W. (1984) Parasites and predators. In: *New Zealand pest and beneficial insects* (R.R. Scott., Ed). Lincoln University College of Agriculture, Canterbury, New Zealand, pp 271-308.

Godfray, H.J.C. (1994) Parasitoids, behavioural and evolutionary ecology. Princeton University Press, New Jersey, USA.

Green, O. R. (1984) New Zealand host and locality records for an introduced tortricid parasite, *Trigonospila brevifacies* (Diptera: Tachinidae). *New Zealand Entomologist* **8**: 69-71.

Howarth, F.G. (1991) Environmental impacts of classical biological control. *Annual Review of Entomology* **36**: 485-509.

Holt, R.D., Lawton, J.H. (1993) Apparent competition and enemy free space in insect host parasitoid communities. *American Naturalist* **142**: 623-645.

M.A.F., 1975: *Monthly Circular, January 1975*. Auckland Plant Health and Diagnostic Station.

M.A.F., 1976: *Monthly Circular, March 1976*. Auckland Plant Health and Diagnostic Station.

Mckenzie, R. J. M., 1981: *Xanthopimpla rhopaloceros*. *Forest Biology Observer*, monthly report for March 1981, south-west Rotorua.

Memmott, J., Godfray, H.C.J., Gauld, I.D. (1994) The structure of a tropical host-parasitoid community. *Journal of Animal Ecology* **63**: 521-540.

Munro, V.M.W. (1997) *Eutorna phaulocosma* Meyrick (Lepidoptera: Oecophoridae), a new host for the introduced Australian parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae). *New Zealand Entomologist* **20**: 71-72.

Murdoch, W.W., Briggs, C.J., Nisbett, R.M. (1996) Competitive displacement and biological control in parasitoids: a model. *American Naturalist* **148**: 807-826.

Odum, E.P. (1983) Basic Ecology. Saunders College Publishing, New York, USA.

Rejmanck, M., Stary, P. (1979) Connectance in real biotic communities and critical values for stability of model ecosystems. *Nature* **280**: 311-313.

Roberts, L. I. N. (1986) The practice of biological control - implications for conservation, science and community. *The Weta* **9**: 76-84.

Salmon, J.T. (1980) The Native Trees of New Zealand. Reed Books, Auckland, New Zealand.

Settle, W.R., Wilson, L.T. (1990) Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. *Ecology* **71**: 1461-1470.

Shaw, M.R., Askew, R.R. (1976) Ichneumonidae (Hymenoptera) parasitic upon leaf-mining insects of the orders Lepidoptera, Hymenoptera and Coleoptera.. *Ecological Entomology* **1**: 127-133

Singh, P. (1983) A general purpose laboratory diet mixture for rearing insects. *Insect Science and its Application* **4**: 357-362.

Thomas, W.P. (1989) *Epiphyas postvittana*, the lightbrown apple moth, in *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 187-195.

Wearing, C.H., Thomas, W.P., Dugdale, J.S. & Danthanarayana, W. (1991) Tortricid pests of pome and stone fruits, Australian and New Zealand species, in *Tortricid Pests, Their Biology, Natural Enemies and Control* (van der Geest, L..P.S. & Evenhuis, H.H., Eds). Elsevier Science Publishers B.V, Amsterdam, The Netherlands. pp 453-472.

Woutts, W.M. (1984) Nematode parasites of lepidopterans. In: *Plant and Insect Nematodes* (Nickle, W.R., Ed). Marcel Decker Inc., New York, USA. pp 655-696.

Life history data for the Australian parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae): is superparasitism adaptive in this species and under what conditions does it occur ?

ABSTRACT:

Life history data for *Trigonospila brevifacies,* a tachinid parasitoid of concealed feeding lepidopteran larvae, were recorded under laboratory and field conditions to determine the frequency at which superparasitism occurs, when superparasitism occurs and if superparasitism is adaptive for this species. Female *T. brevifacies* live for an average of 30 days, with a pre-ovipositional period of six days, and parasitise approximately 83 hosts in a lifetime. Most of the macrotype eggs are laid on the three thoracic segments of its late-instar larval hosts. At 18±2°C, development time from oviposition to adult emergence averaged 38 days. The sex ratio of progeny was 1:1. Under laboratory conditions, almost 30% of females failed to oviposit or laid infertile eggs. In the field female *T. brevifacies* were frequently observed ovipositing throughout the summer, autumn and late spring months.

Self-superparasitism occurred on 54% of hosts in the laboratory and 48% of larvae collected from the field carried multiple eggs oviposited by one or more females. Self-superparasitism and superparasitism of hosts resulted in smaller adult progeny. However, no significant relationship was found between adult female size and lifetime productivity. The strategy of laying multiple egg clutches was shown to be an adaptive for *T. brevifacies* when host density is low. Superparasitism in the field was not significantly more prevalent during any particular season. Increased levels of superparasitism were negatively correlated with host densities at field sites. Therefore, superparasitism appears to function as a strategy which increases the mean number of progeny a female can produce, when hosts are less abundant. Superparasitism may not be a desirable characteristic in parasitoid species used for biological control, but may lead to a reduced impact on rare non-target hosts in native habitats.

INTRODUCTION:

Trigonospila brevifacies (Hardy) (Tachinidae) was introduced to New Zealand from Australia as a biological control agent against orchard pest tortricids 30 years ago. This species is of

particular interest to biological control practitioners because it has been found to parasitise non-target native tortricids. Little quantitative work has been carried out in Australia or New Zealand concerning the biology, behaviour or ecology of the parasitoid. The aim of this work was to quantify the life history parameters and describe the reproductive behaviour of *T. brevifacies* under laboratory conditions. Such information is relevant to the formation of predictions about the impact of *T. brevifacies* on non-target lepidopteran hosts in the native habitats which it has invaded since its release in New Zealand.

Early (1984) described *T. brevifacies* as a yellow and black-banded solitary tachinid which parasitises late-instar lepidopteran larvae. Macrotype eggs are deposited by the adult female on the head and thorax of host larvae that have emerged from their leaf shelters. It is normally a larval-larval parasitoid (where a parasitoid egg is laid on a larval host and the parasitoid larva emerges from the host prior to pupation), but does sometimes present as a larval-pupal parasitoid (where eggs are laid on a larval host, but the mature parasitoid larva emerges from a host that has begun pupating). After the parasitoid larva emerges from its host, it pupates inside the host's leafshelter (Thomas, 1975).

Godfray (1994) defines self-superparasitism as when a female lays an additional egg or eggs on a host that she has parasitised in a previous ovipositional bout. Superparasitism occurs when a female oviposits on a host that has been previously parasitised by a conspecific. van Alphen and Nell (1982) were first to recognise it as an adaptive strategy. The function of superparasitism, invoking Lack's solution, is to produce an optimal number of progeny that will maximise female fitness (see below, p 99) (Lack, 1947). *Trigonospila brevifacies* exhibits self-superparasitism under laboratory conditions and hosts with multiple *T. brevifacies* eggs (either superparasitism or self-superparasitism) are frequently collected in the field (Early, 1984).

Several factors have been demonstrated either by models or empirical work to be costs of superparasitism. These are 1) wastage of eggs when additional eggs do not result in any additional progeny (Hubbard *et al.*, 1987), 2) reduced fecundity of smaller female progeny (Waage & Ng, 1984; Hardy *et al.*, 1992) and reduced competitiveness of smaller male progeny (Adamo *et al.*, 1995), 3) the risk that additional parasitisms may result in host death before parasitoid larvae finish development (Munro, unpub. data), and 4) the cost of handling time associated with superparasitising a host which may return fewer mean progeny per egg than an unparasitised host (van Alphen & Visser, 1990).

Superparasitism is adaptive when 1) the pay-off of an additional egg has a greater than zero chance of producing progeny (Visser *et al.*, 1992), 2) when parasitoids are short-lived and unparasitised or preferred developmental stage hosts are rare (van Baaron *et al.*, 1995), 3) when the risk of conspecific superparasitism within a patch is high (van Alphen & Visser, 1990), 4) when the cost of travel between distantly spaced prey patches is high (van Baaron *et al.*, 1995), or 5) when primary parasitisms are used to exhaust host immune defence responses allowing secondary parasitisms to be successful (van Alphen & Visser, 1990).

Fitness can be measured by the size, rate of development, longevity and lifetime productivity (e.g., eggs laid, number of hosts parasitised) of adults. Self-superparasitism is non-adaptive in some parasitoid species when it results in competition between siblings within a host and only one adult is able to develop (van Alphen and Visser, 1990). Superparasitism is non-adaptive when an interval of several hours between the primary and secondary ovipositions limits the likelihood of the second oviposition being successful (Visser *et al.*, 1992; Adamo *et al.*, 1995; van Baaron *et al.*, 1995), when hosts are abundant, or when the mean number of progeny from a clutch of multiple eggs is less than that of a host bearing a single oviposition (van Alphen and Visser, 1990).

Both host availability and parasitoid condition initiate the use of this strategy. Godfray (1994) reviewed empirical work which indicates conditions under which superparasitism is likely to occur. Superparasitism in parasitoids occurs when encounter rate with parasitised hosts is high (Visser *et al.*, 1992), the number of conspecific females searching a host patch is high (Visser *et al.*, 1992), female egg load is low (Volkl & Mackauer, 1990). Superparasitism can also be dependent on; female age (Takasu & Hirose, 1991), and female size (Collins & Dixon, 1986). Visser *et al.* (1992) also speculated that superparasitism may occur in parasitoids that have imperfect host discrimination because they have not evolved a mechanism to mark hosts at the time of parasitism.

Data were gathered on the reproductive capabilities of *T. brevifacies* both in the field and laboratory. The ultimate aim of this work was to determine the frequency with which superparasitism occurs and whether it might be an adaptive reproductive strategy for *T. brevifacies*. The potential advantages and disadvantages of a parasitoid biocontrol agent exhibiting superparasitism in target and non-target host populations are also discussed.

METHODS:

Laboratory experiments

A population of *T. brevifacies* (100 females and 100 males) was founded from adult tachinids and parasitised hosts collected from native forest in three North Island regions (Bay of Plenty, Wairarapa and Manawatu). The founder colony was provided with 4th-5th instar *Ctenopseustis obliquana* (Walker) (Lepidoptera: Tortricidae) larvae on the native shrub mahoe (*Melicytus ramiflorus* Forster) for four hours daily over a six week period. Parasitised larvae were held individually in vials with a general purpose tortricid diet (Singh, 1983) until the parasitoid larva emerged and pupated.

The gender of newly emerged adult parasitoids was determined and the body length measured with an eyepiece micrometer. As parasitoid wings were occasionally damaged, body length was chosen as a measure of adult size rather than the more widely used measurement of wing length.

The lifetime productivities of 115 newly emerged adult *T. brevifacies* females were recorded. Lifetime productivity is defined as, the number of eggs oviposited by females that successfully produced live adult *T. brevifacies* progeny. Seventy females were given the opportunity to oviposit, with a control group of 45 females caged under duplicate conditions except that they were never provided with hosts.

Each newly emerged female was placed with two males in a cylindrical clear plastic Click Clack ™ food container (30 cm by 24 cm). Ventilation was provided by a 10 cm diameter hole in the top of the container, which was covered by 5 µm nylon mesh. All cages were provided with cotton wool moistened in distilled water and 0.05 grams of honey-agar parasitoid diet (recipe Insect Rearing Unit, Hort Research) on a petri dish. Field and laboratory observations had previously shown that once a host is located, the mean oviposition time per egg, per host for a female *T. brevifacies* is about 70 minutes (Munro, unpub. data). These trials also indicated that a single female did not parasitise more than eight hosts per day under laboratory conditions. As a result of these data, each cage was provided with ten, fifth-instar *C. obliquana* hosts every 24 hours. At the end of each 24 hour period, host larvae were inspected and the number of eggs laid and larvae parasitised were recorded until females died. Cages were kept in temperature

controlled (18± 2°C) laboratory conditions with uncontrolled humidity and a 16:8 h photoperiod.

Ctenopseustis obliquana hosts were chosen as the host species for this work as it is a common host of *T. brevifacies* in the field (Chapter 3). Fifth-instar *C. obliquana* larvae were reared by the Hort Research Insect Rearing Group, at Mt. Albert, Auckland, in tubes containing artificial diet (GPD) (Singh 1983). In order to replicate natural conditions as closely as possible, host larvae were presented to *T. brevifacies* in leaf shelters. *Melicytus ramiflorus* was chosen as a suitable host plant for *C. obliquana* as it is frequently collected from this native shrub in the field. This plant/host combination accounted for 31 % of parasitisms by *T. brevifacies* of larvae collected over two years from native habitats in three North Island regions (Chapter 3).

Two 8 cm long leaves of *M. ramiflorus* were fastened together with a pin along one edge of the leaves. A single fifth-instar larva was then introduced into the leaves. Each leaf shelter with its larva was then inserted into a moistened rectangle of florists oasis (12 cm long, 5 cm wide, 4 cm deep), to keep the leafshelters fresh. Soon after placement, caterpillars further secured their individual leaf shelters with silk and began to feed on the shelters.

At the end of each twenty-four hour period of exposure all leaf shelters were removed from the cages and larvae were checked for *T. brevifacies* eggs (eggs are visible to the naked eye). Parasitised larvae were removed daily, but unparasitised larvae were put in new leaf shelters and returned to the cages with each female *T. brevifacies*, extra larvae were added to make the host number up to 10 per cage again. Each day the number of larvae parasitised per female, the number of eggs per larva and the position of eggs on each host were recorded. After these records were taken, parasitised larvae were assigned an individual code and placed individually in glass rearing tubes with artificial diet. Stages of development were noted daily until a *T. brevifacies* pupa formed or a *C. obliquana* moth emerged.

Life history data gathered included longevity, length of pre-ovipositional period, number of egg-laying days, eggs laid per day/lifetime, occurrence of self-superparasitism, larvae parasitised per day/lifetime, lifetime productivity (percentage of ovipositions that resulted in the emergence of adult *T. brevifacies*), development time, sex ratio of progeny, adult progeny size and male longevity.

Field surveys of superparasitism

Data on superparasitism were gathered in seasonal surveys at six North Island sites in the entomological regions of Bay of Plenty, Manawatu and Wairarapa. The methods are reported in Chapter 3. An index of host density was calculated using the time taken on each sampling occasion to collect 40 host larvae along two 40 m transects, with samples taken at two metre intervals.

Field cage experiments

The life stage in which *T. brevifacies* overwinters and the time taken for a host parasitised in autumn to develop into an adult parasitoid were unknown. A field cage (4m x 3m x 2m) constructed of fine nylon mesh was used to assess overwintering. Ten 1.5 m high potted *M. ramiflorus* were placed in the field cage. In April 1997 ten late-instar *C. obliquana* larvae were placed on each shrub. Forty-eight hours later when larvae had constructed leafshelters, five female and five male *T. brevifacies* adults were released into the field cage. A week later this process was repeated with more *T. brevifacies* and hosts. Daily inspections of leafshelters were conducted to determine whether 1) parasitism had occurred, 2) parasitoid larvae had invaded their hosts, 3) when the parasitoid larvae had pupated, and 4) adult parasitoids had emerged.

Field observations

Weekly field observations in the Manawatu and Wairarapa were made throughout the year in 1996 and 1997 to determine when *T. brevifacies* was active. Observations of male basking and of ovipositing females or parasitised host larvae were noted.

Data analysis

The associations between adult progeny size, the number of progeny produced per host and the number of eggs laid per host, were evaluated using Analysis of Variance in SYSTAT (Wilkinson, *et al.*, 1996). Means were compared using a Posthoc Tukey test. Chi-square analysis was used to determine whether the sex ratio of progeny differed between single and multiple progeny. Potential costs of self-superparasitism were explored by assessing the correlation between female size, total number of eggs laid, and longevity.

Whether self-superparasitism is an adaptive reproductive strategy in *T. brevifacies* was assessed by estimating the relative success of laying more than one egg per host. This was achieved by calculating the mean number of progeny per egg laid from the 4,000 progeny produced in the laboratory. Poisson distributions were used to calculate the relative benefits of

female *T. brevifacies* adopting a random egg laying strategy compared to laying one, two, three or four egg clutches at different host densities. The profitabilities of various clutch sizes were calculated from laboratory and field data, and were plotted to define the trends in SYSTAT .

The frequency of multiple egg laying and number of multiple progeny were calculated as a percentage from field and laboratory data. The association between host density and levels of superparasitism in the field was estimated by calculating the mean number of eggs laid per host larva that was found at each site on each sampling occasion.

RESULTS:

Life history and lifetime productivity data

Female *T. brevifacies* were tested to determine mean longevity, realised fecundity (mean number of eggs laid/female) and productivity (mean number of live adult progeny to emerge) measures. Development and generation length data were gathered from over 2,500 progeny of tested females.

Life history data for *T. brevifacies* reared on *C. obliquana* under laboratory conditions are presented in Table 1. Males, control females and test females all lived for approximately 30 days. Females had a pre-ovipositional period of about six days and oviposited for a mean of 21 days. There were typically no ovipositions made for an average of three days prior to death. *Trigonospila brevifacies* eggs took approximately three days to hatch. The parasitoid larva spent 13 days feeding endogenously on the host prior to emergence and pupation beside the host or within the cadaverous remains or pupal husk of the host. The pupal stage took 21 days at 18± 2°C.

Lifetime productivity data for *T. brevifacies* under laboratory conditions are presented in Table 2. The mean number of eggs laid per female ($n = 70$) was 185 and an average of 88 hosts were parasitised per female lifetime. The daily rate of oviposition was greatest between day 7 and 15, with a maximum mean of 11 eggs laid in a 24 hour period (Fig. 1). Females oviposited from 6 days old to a maximum of day 55. The mean number of hosts parasitised per female followed a similar pattern. A mean maximum of 5 hosts parasitised per female per day was recorded on day 12 (Fig. 2). However, on occasions up to 8 larvae were parasitised by some females in a 24 hour period.

Table 1. Mean life history data for *Trigonospila brevifacies* reared on *Ctenopseustis obliquana* at 18±2°C.

	Longevity ovipositing female (days)	Longevity non-ovipositing female (days)	Male longevity (days)	Pre-ovipositional period (days)	Ovipositional period (days)	Juvenile development egg → pupa (days)	Juvenile development pupa → adult (days)
Mean	30.67	34.3	30.8	6.47	21.46	16.25	21.81
Std dev	± 18.25	± 24.9	± 16.8	± 3.39	± 13.87	± 2.24	± 3.21

Table 2. Mean lifetime productivity per female *Trigonospila brevifacies* reared on *Ctenopseustis obliquana* at 18±2°C.

	Number eggs laid	Number hosts parasitised	Number male adult progeny	% adult progeny male	Number female adult progeny	% adult progeny female	Productivity measures (% hosts → adult fly)	Productivity measures (% eggs→ adult fly)
Mean	185.03	88.43	29.83	49.02	33.46	51.00	76.26	36.60
Std dev	± 108.83	± 52.47	± 19.42	± 7.41	± 19.1	± 6.86	± 19.40	± 10.61

Table 6. Success of multiple egg laying strategy self superparasitism by *T. brevifacies* in the laboratory at 18±2°C.

	% occurrence of multiple egg clutches per female	mean number of eggs laid on superparasitised hosts	% failure*of single egg clutches	% failure of multiple egg clutches (>1 egg per host)	% multiple egg clutches producing >1 adult parasitoid progeny	% occurrence of multiple adult progeny, of total progeny per female
Mean	54.75	3.95	29.38	15.58	13.53	8.30
Std dev	± 10.85	± 2.10	± 18.40	± 13.02	± 6.51	± 4.91

* failure = failure to produce any adult progeny.

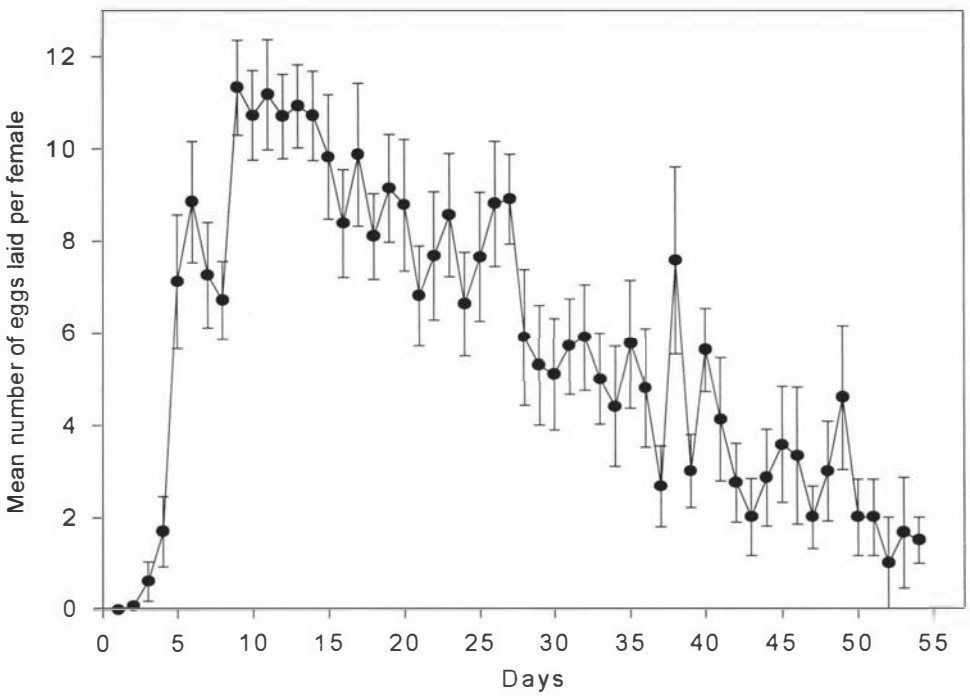


Figure 1. Mean lifetime productivity of female *T. brevifacies* under laboratory conditions at 18± 2°C.

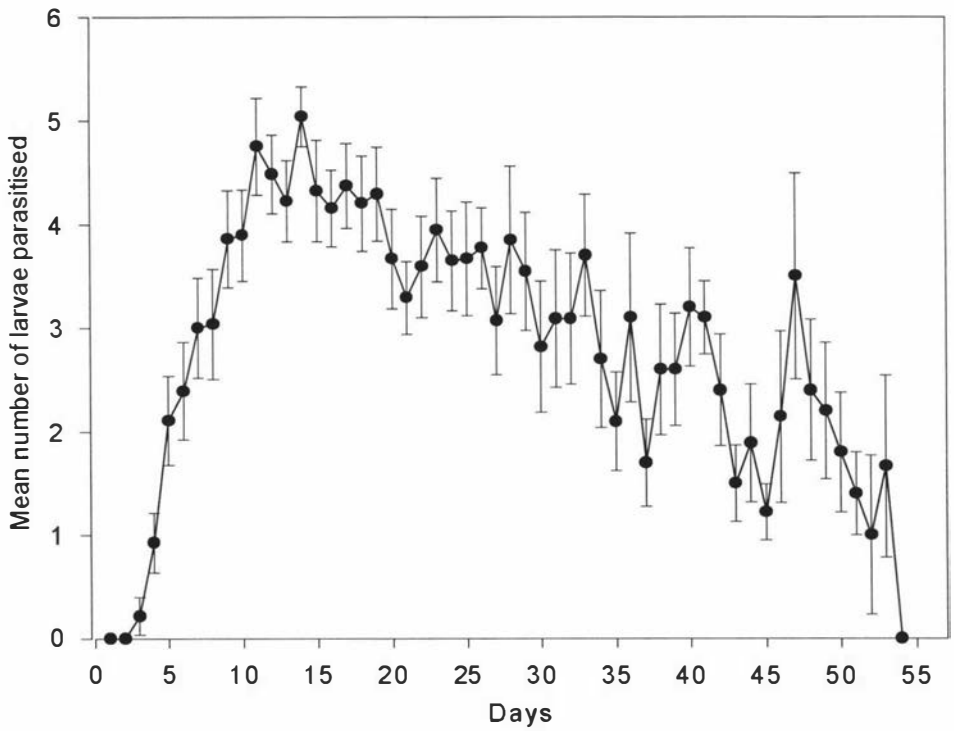


Figure 2. Mean lifetime productivity of female *T. brevifacies*, daily parasitism levels under laboratory conditions at 18± 2°C.

The majority of ovipositions (78%) occurred on the thoracic segments of hosts, with no preference for either dorsal, ventral or lateral aspects. Remaining ovipositions occurred on the head and abdominal regions of hosts (Fig. 3), particularly when these areas were exposed to an ovipositing parasitoid due to damage to the leaf shelter by larval feeding activity. The sex ratio for *T. brevifacies* adult progeny was 49 % males and 51 % females. Seventy-six percent of parasitised hosts produced adult parasitoid progeny, with successfully ovipositing female *T. brevifacies* producing on average 63.3 adult offspring.

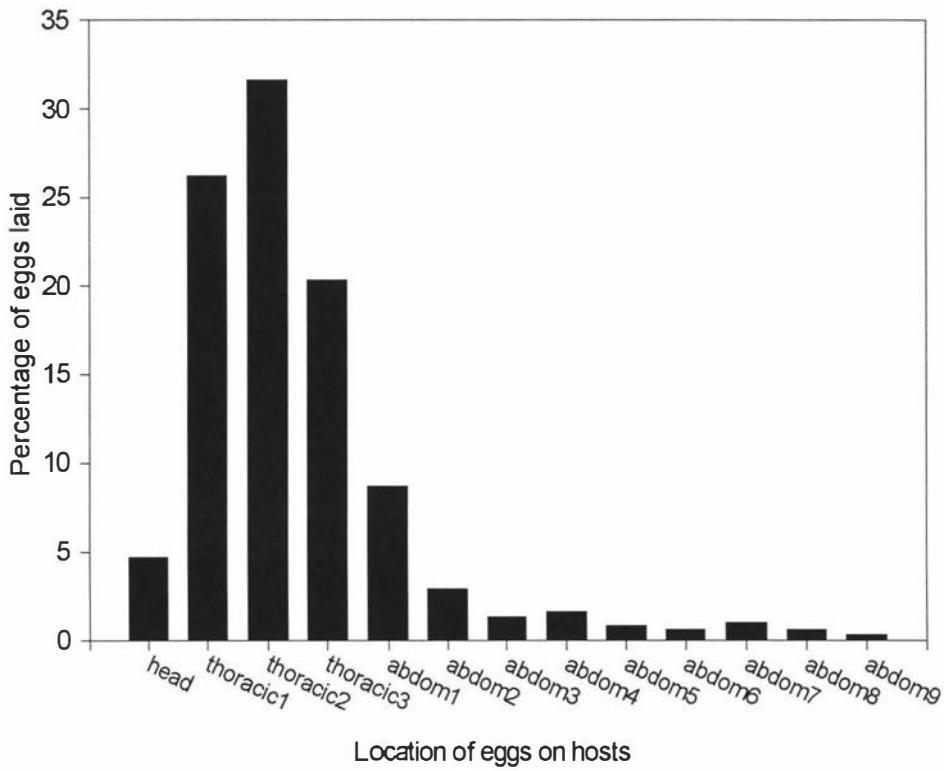


Figure 3. The location of *T. brevifacies* eggs laid on the segments of larval hosts (n = 4,934).

Several mortality factors were identified under laboratory conditions that accounted for the 63.4 % loss in potential productivity detected in this parasitoid species. Highest mortality occurred in the parasitoid egg stage (34 %). Some eggs were moulted with host exuviae before they could hatch in the laboratory. This also occurred with field collected hosts, but some eggs failed to hatch on the host after the usual 3 days. Mortality also occurred in the larval stage when larvae killed the host before the parasitoid had completed development. In some cases, development of the parasitoid larvae stopped without obvious cause. In other instances,

hatched parasitoid eggs were observed on the hosts body and parasitoid larvae could be seen through the hosts integument, but failed to kill the host which later successfully developed into a moth. It is possible that the host's immune defense system killed the parasitoid larva. The cause of the 6.4 % failure of parasitoid puparia to produce adult *T. brevifacies* is also unknown. Of females tested, 37 % either failed to oviposit or all eggs oviposited were infertile (Table 3).

Table 3. Limitations to productivity of female *T. brevifacies* under laboratory conditions at 18± 2°C.

Life stage	cause	mean mortality of parasitoid larvae
egg	shed with instar moult or infertile (parasitised larvae later developed into moths)	33.82 %
larvae	host death or host immune defenses attack parasitoid larva	23.14 %
puparia	adult fly failed to develop in puparia (cause unknown)	1.64 %
	developed adult fly failed to emerge from puparia (cause unknown)	4.80 %
total mean mortality		63.40 %

Infertility	Sample size	% infertility
Percentage of females tested who never oviposited	70	28.6
Percentage of females tested whose eggs were all infertile	70	8.6

In the field cage experiment, all development stages were longer than those observed in the laboratory, although no diapause was observed and parasitoid larvae formed puparia even in winter (Table 4).

Table 4. Comparison of development time of parasitoids overwintering in field cage or laboratory conditions

	Temperature range	Mean development time egg-adult
Winter field cage	-3°C to 16°C	116 days
Laboratory	18± 2°C.	38 days

Male *T. brevifacies* were observed basking on vegetation in the field during sunny periods in eight months of the year, individuals were also seen on winter mornings after overnight frosts of ˉ2°C. However, female activity appeared to be confined to summer, autumn and late spring (Table 5).

Table 5. Monthly field observations of *Trigonospila brevifacies* activity (1996-98).

Month	Male leking	Female ovipositing
January	✓	✓
February	✓	✓
March	✓	✓
April	✓	✓
May	✓	✓
June		
July	✓	
August	✓	
September		
October		
November	✓	✓
December		✓

Superparasitism in laboratory and field environments

Superparasitism was frequently recorded under laboratory and field conditions and the level of incidence was similar in the two environments. Multiple progeny from superparasitised hosts occurred in 7% of hosts collected from the field and 8.3% of hosts parasitised in the laboratory. Self-superparasitism occurred on 54.7% of hosts in the laboratory and superparasitism in 47.9% of field samples. In the laboratory, the mean size of multiple egg clutches were of 2 eggs per host. In the field the mean number of eggs per clutch was 1.67 eggs. Multiple eggs laid on a host resulted in a lower mean level (15.6%) of failure (where failure is defined as an adult parasitoid does not result when an egg or eggs are successfully laid on a host) than a host with a single egg (29.4%) when calculated for all females tested (Table 6).

The size of adult progeny produced was negatively related to the number of eggs laid per host by ovipositing females ($F_{9,1756}$ =13.1, P<0.00001) (Fig. 4). The size of adult progeny also declined with increasing numbers of progeny per host ($F_{3,1768}$ = 240.1, P<0.00001) (Fig. 5). A Posthoc Tukey pairwise comparison test indicated that the size of adult progeny in the multiple progeny categories were significantly different, except between the 2 and 3 progeny per host groups. Gender was added to the model to test the effect of clutch size on adult progeny size. There was a significant interaction between clutch size and gender ($F_{9,1756}$ = 3.71, P<0.0005): as clutch size increased the size difference between male and female *T. brevifacies*

decreased (Fig. 6). There was also a significant interaction between gender and the number of progeny per host ($F_{3,1768} = 9.11$, $P<0.00001$), as the number of adult progeny to emerge from a host increased the difference between the size of male and female progeny decreased.

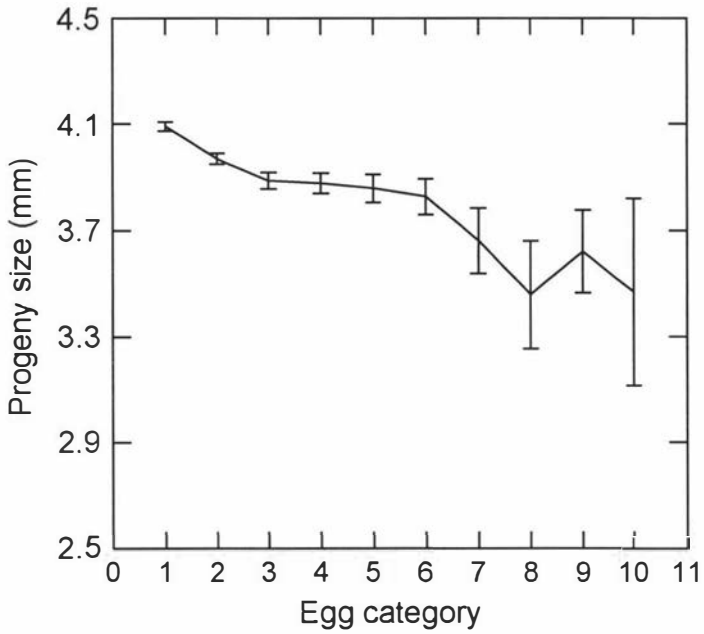


Figure 4. The relationship between the size of *T. brevifacies* adult progeny (± SE) and the number of eggs per host *C. obliquana*.

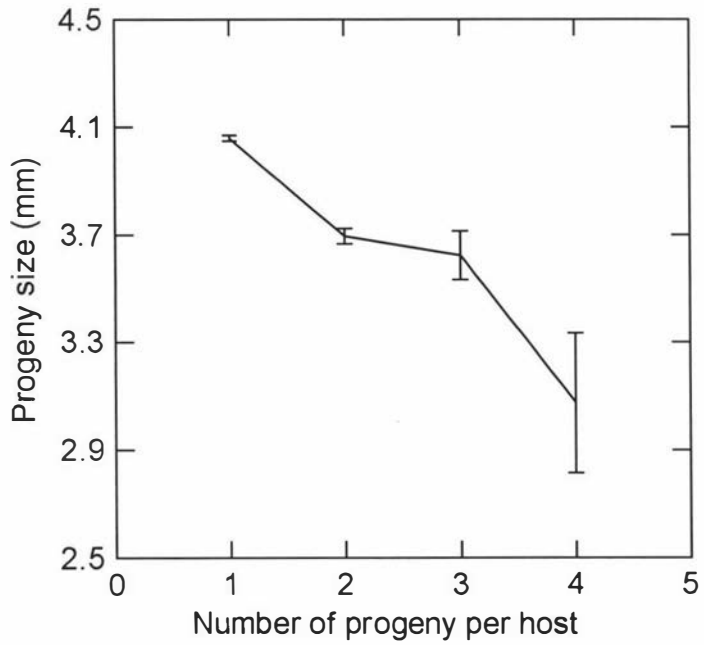


Figure 5. The relationship between the size of *T. brevifacies* adult progeny (± SE) and the number of progeny per host *C. obliquana*.

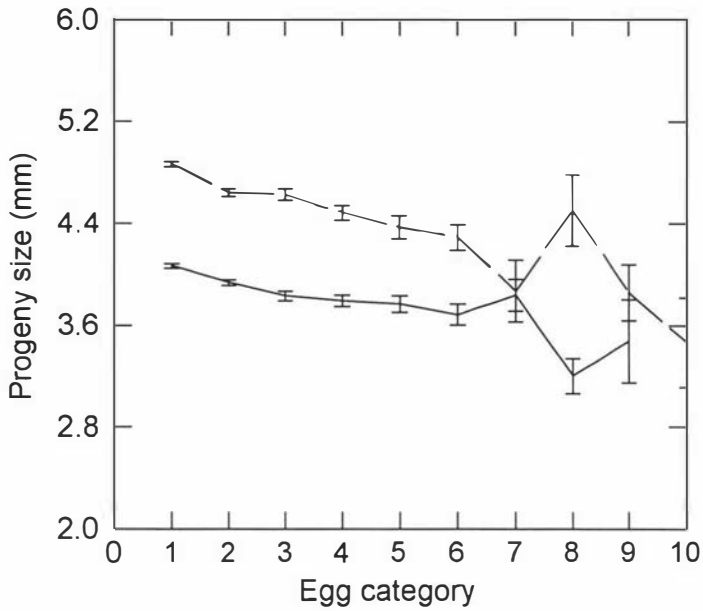


Figure 6. The relationship between the size of adult male and female *T. brevifacies* progeny (± SE) and the size of egg clutches per host *C. obliquana*. Genders are shown as males - - - - and females ____ .

Four measurements were made to determine whether smaller progeny incurred fitness costs: the number of eggs laid, the number of hosts parasitised per female lifetime, female longevity and the rate at which females laid eggs. Adult female size did not significantly affect the number of eggs oviposited per lifetime (R= -0.136, P=0.472) or the number of hosts parasitised per lifetime (R = -0.248, P=0.187), but there was a negative correlation between number of oviposition days and female size (R= -0.397, P=0.084), i.e., small females oviposited the same number of eggs and parasitised the same number of hosts but laid their eggs at a slower rate than larger females (R= -0.397, P=0.30). Another potential cost imposed by self-superparasitism is a deviation in the sex ratio of multiple progeny compared to single progeny. However, the ratio of male to female progeny was not significantly different among clutch size categories (1-8+) (χ^2_7= 2.49, P=0.93) nor adult progeny per host categories (1-3+) (χ^2_2= 4.12, P=0.13).

Laboratory and field data were used to determine the relative success (measured as the mean number of adult progeny per host) of each additional egg laid on a previously parasitised host. Clutch size was determined by visual inspection for both field and laboratory samples. Because egg husks remain on the host body for several days after the parasitoid larva has emerged, enabling accurate assessment of field egg clutches is possible. Both parasitised hosts

collected from the field and caterpillars parasitised in the laboratory were reared under the same conditions. The trends of increasing productivity with increasing egg clutch sizes were found to be similar for laboratory and field data. The frequency of clutch size distribution was not significantly different between field and laboratory data ($\chi^2_3 = 0.285$, P=0.963). Single eggs comprised 48.3% and 45.3 % of clutches, two-egg clutches 25 % and 27.8 %, three-egg clutches 13.3 % and 13.5 %, and four or greater egg clutches 13.3 % and 13.26 % on samples from the field and laboratory, respectively. However, some differences were found between the two data sets. Single and multiple egg clutches obtained from the field produced consistently more adult progeny per egg than those obtained in the laboratory (Table 7). The trends in productivity with increasing clutch size are graphed for laboratory (Fig. 7a) and field (Fig. 7b) data sets.

Table 7. The mean number of *T. brevifacies* adult progeny produced per clutch size.

Clutch size	Number of progeny produced					Total eggs	Mean progeny per clutch
	0	1	2	3	4		
Laboratory data							
1	474	603	-	-	-	1077	0.56
2	217	395	49	-	-	661	0.745
3	83	200	34	4	-	321	0.87
4	26	114	17	2	1	160	0.99
5	15	50	13	4	-	82	1
6	5	24	4	1	-	34	1.05
7	3	11	5	-	-	19	1.1
8	1	4	2	-	-	7	1.1
9	2	2	3	1	-	8	1.18
10	1	-	1	-	-	2	1.18
11	1	-	-	-	-	1	1.19
12	1	-	1	-	-	2	1.2
13	-	-	1	-	-	1	1.2
14	1	-	-	-	-	1	1.2
Field data							
1	7	22	-	-	-	29	0.76
2	6	20	4	-	-	30	0.84
3	3	18	6	-	-	27	1.11
4	4	12	4	-	-	20	1.20
5	-	1	1	-	-	10	1.50
6	-	-	1	-	-	6	1.98

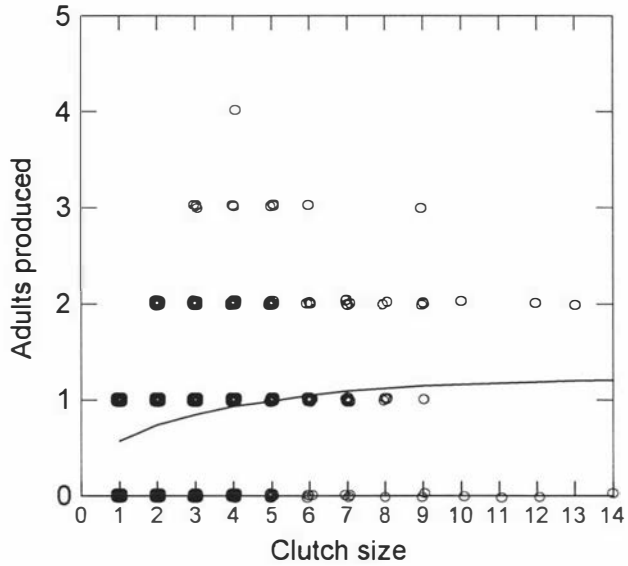


Figure 7a. Adult *T. brevifacies* produced (mean number of adult progeny per egg) from various egg clutch sizes, in the laboratory at 18 ± 2°C. Lowess smoother applied to line.

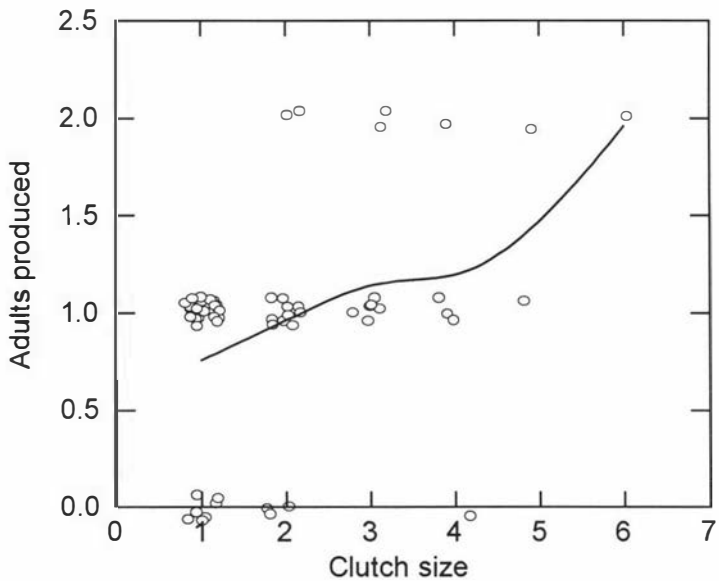


Figure 7b. Adult *T. brevifacies* produced (mean number of adult progeny per egg) from various egg clutch sizes in the field. DWLS smoother applied to line.

Multi-season data were used to determine when superparasitism was occurring in the field. No significant difference was found in the number of *T. brevifacies* eggs recorded per host during any sampling occasion, nor among seasons (spring, summer, autumn) ($F_{6,10}$=0.99, P=0.48). However, the level of superparasitism (mean number of eggs laid per host per sampling occasion) was negatively correlated with larvae found per unit of search time (R=.545, P=0.023) (Fig. 8).

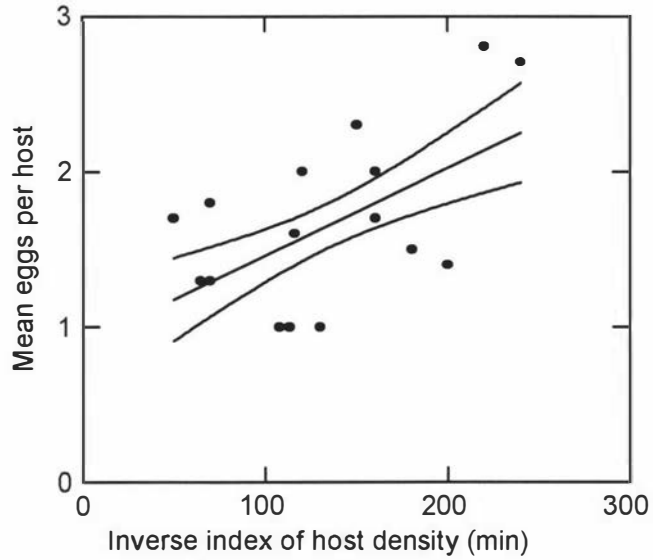


Figure 8. Relationship between the mean number of *T. brevifacies* eggs laid per host and host density. Host density was determined as the time taken to collect 40 caterpillars and is represented as an inverse index of host density.

Laboratory data were used to calculate the relative success of adopting a random egg laying strategy compared to single egg clutches and superparasitism strategies of two, three or four egg clutches at various hypothetical host abundances. The model assumed that females have a maximum of 100 hosts available to them and could not modify their behaviour. When hosts were rare (less than 25), a female *T. brevifacies* laying four-egg clutches gave the highest mean number of progeny per egg laid and there was a low pay-off for females laying single egg clutches who retained eggs at low host densities. At medium host abundances (50 hosts) females laying two-egg clutches or adopting a random strategy had the highest mean number of adult progeny. At levels of high host abundance (100 hosts) single or random egg laying are the best strategies (Fig. 9). Therefore, when hosts are rare or moderately abundant the most productive strategy for *T. brevifacies* females is to superparasitise and when hosts are abundant the best pay-off per egg is to lay single egg clutches.

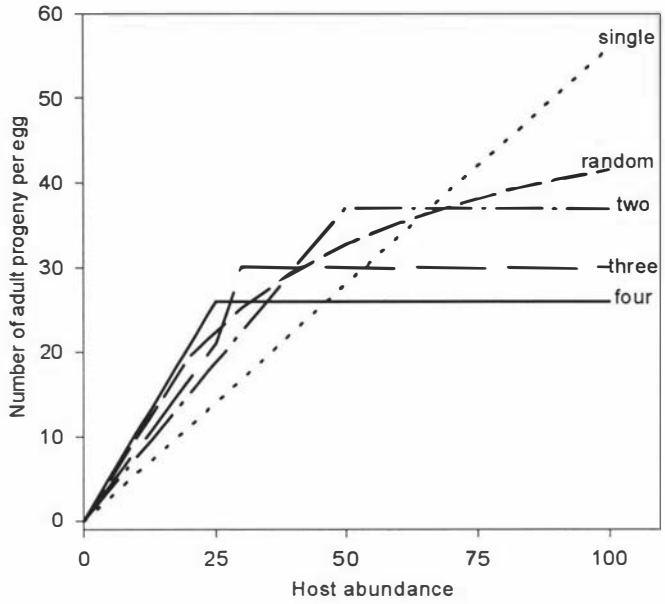


Figure 9. Relative success of single multiple and random egg laying strategies by *T. brevifacies* at different host densities. Productivity values for random clutches are generated using Poisson distributions.

DISCUSSION:

Life history

Trigonospila brevifacies is a species that has characters that are intermediate between those mentioned in definitions of solitary and gregarious parasitoids (see Speirs *et al.*, 1991). It oviposits single eggs and therefore produces single progeny per host in almost half of the field and laboratory samples recorded. However, superparasitism of hosts may, at times, produce up to four progeny per host. This intermediate reproductive behaviour in parasitoids is rare (Godfray, 1987; Moratorio 1987).

The majority of *T. brevifacies* eggs are deposited on the thorax of hosts. Herrebout (1969) speculates that this behaviour has evolved in some tachinid species to avoid egg mortality by larval host grooming. Alternatively, it may simply be that hosts that occupy leaf shelters expose only their head and thoracic regions when feeding, and therefore only make these areas available for oviposition by parasitoids which oviposit onto the host integument (Belshaw, 1993).

The longevity of female *T. brevifacies* is similar to the developmental time for its common leafroller host *Planotortrix octo* (Walker) at 18°C under laboratory condition (D.J. Rogers, unpub. data, 1997). However, *T. brevifacies* females can be collected from the field at any time from late spring to late autumn and its polyphagous habits and wide host range does not require synchrony with a particular host species. Also, the most frequent hosts of *T. brevifacies* in New Zealand are Tortricidae which are multivoltine (Wearing *et al.*, 1991).

Benefits of superparasitism and *T. brevifacies*

Levels of superparasitism recorded in the field corresponded closely with those found in the laboratory. About half the parasitised hosts were superparasitised in both environments. Of hosts bearing multiple egg clutches, 7% produced more than one adult parasitoid in the field and 8% in the laboratory. Failure of single egg clutches to produce adult *T. brevifacies* occurred in 44 % of cases, while two or more egg clutches had more successful outcomes. Therefore, the investment in multiple egg clutches has two pay-offs; increasing the probability that 1 progeny will result per host and providing a chance that two progeny will result per host. Although the frequency of clutch sizes and trends in productivity for laboratory and field data agreed, some differences existed in the degree of productivity per egg. The mean number of progeny expected from each clutch size was consistently higher in the field. This difference

could arise if the time between ovipositions was shorter and the age of parasitoid larvae closer for field parasitisms. In the laboratory, the time between individual eggs being laid was constrained by the time it took a single female to successfully oviposit and then lay a second egg. In the field two females may have oviposited on a host rapidly one after the other, therefore parasitoid larvae would be of similar ages and so the mean number of adult progeny per egg increases. Parasitoid larvae are able to compete more successfully if they are of similar ages because larval competition and siblicide is reduced within a clutch (Visser *et al.*, 1992; Adamo *et al.*, 1995). Therefore, if the time between *T. brevifacies* ovipositions in the field is shorter it may result in greater productivity per egg laid.

Direct costs of superparasitism

Size, longevity and lifetime productivity were chosen as indicators to test whether superparasitism has an impact on the fitness of *T. brevifacies* progeny. *Trigonospila brevifacies* progeny of superparasitised hosts were smaller than single progeny. However, no direct costs to longevity or productivity were detected in smaller individuals of this species, nor were the sex ratios of *T. brevifacies* progeny significantly different between any of the clutch size categories. Smaller females lived longer than larger females, but laid the same number of eggs because eggs were laid at a slower rate in the laboratory. No direct cost was found to be associated with being a small female of a multiple egg clutch.

Indirect costs of superparasitism

Godfray (1994) emphasised that laboratory experiments measuring the relationship between fitness and size in parasitoids are likely to underestimate the fitness costs to small individuals. No direct costs to small female *T. brevifacies* were detected under laboratory conditions in the present study. However, indirect costs to small progeny not measured here may ultimately limit the direct advantages of increased productivity for females which superparasitise their hosts. Some factors have been identified as costs to small individuals among parasitoid species, though not necessarily as a result of superparasitism. Petersen (1996) found that smaller female bethylid wasps lost contests for host patches to larger conspecific females.

Male *T. brevifacies* are larger than females and therefore are likely to use more host resources than female progeny. Extrapolating from the Sexy Son Hypothesis (Weatherhead & Robertson, 1979), smaller male progeny, in a species such as *T. brevifacies* where males lek, may not be effective competitors within a lek and gain fewer mates, so providing a lower

fitness pay-off for the foundress female. Adamo *et al.* (1995) speculate that small males of the tachinid *Ormia ochracea* may be unable to successfully compete for mates when competing with larger males in a lek. However, if most *T. brevifacies* males emerging in spring are small, as a consequence of high levels of autumn superparasitism, small males may not be disadvantaged in male-male competition for mates. Some field observations suggest that small emergent male *T. brevifacies* are more abundant in spring (Munro, unpub. data). Therefore, being small among other small males may be less costly to potential fitness. Finally, size may impose limitations on the ability of small individuals to disperse to find mates or search for hosts.

Indirectly a larger female may be better able to exploit short term host abundances. Being a small female, as a result of superparasitism, could also have indirect costs. Dispersal and flight can be important in parasitoids when locating their hosts. Larger females may be stronger fliers and so travel further, therefore they could be better at locating hosts at low densities.

Superparasitism in the field

Mechanisms, such as the marking of hosts and patches with pheromones and egg counting, are used by some hymenopteran parasitoids to avoid superparasitism by conspecifics (van Alphen & Visser, 1990). Askew (1971) stated that no tachinid species is known to be able to discriminate parasitised hosts. Field and laboratory observations also indicate that *T. brevifacies* does not appear to avoid self-superparasitism or superparasitism.

However, field data indicated that superparasitism by *T. brevifacies* is associated with low host densities. Superparasitism is predicted to occur when hosts are rare because superparasitism has a fitness pay-off when search times for hosts are long and if parasitoids are not egg-limited (van Alphen & Visser, 1990). The host-handling time of laying an additional egg is likely to be shorter than the time taken to search for a new host, in species that are not egg limited (Godfray, 1994). Thus, ovipositing on every host found will have a greater pay-off than only ovipositing on unparasitised hosts if secondary eggs produce some increment of return in progeny.

Is superparasitism adaptive in *T. brevifacies* ?

When laboratory data for the productivity of *T. brevifacies* were modelled, they predicted that multiple-egg clutches should be laid when hosts are rare and single egg laying should be

employed when hosts are abundant. Field data supported this prediction. It is not an evolutionary stable strategy to always be a single egg laying female or to always superparasitise (van Alphen & Visser, 1990) and field data indicated that clutches of multiple eggs declined in *T. brevifacies* when hosts were abundant.

This study determined no direct costs to the fitness of an individual female *T. brevifacies* by utilizing the reproductive strategy of superparasitism. Therefore, superparasitism by *T. brevifacies* is an evolutionary stable strategy, and adaptive because it is adopted when hosts are rare. Superparasitism may provide less pay-off (i.e. mean adult progeny per egg) for individual female *T. brevifacies* than determined by the present study, because there may be additional fitness costs associated with being progeny of a multiple egg clutch. These potential costs include; the relative success of additional eggs per host over a latency period between primary and secondary ovipositions and the impact of adult size on conspecific female-female contests for hosts and patches and male-male contests for mates.

Superparasitism and its potential consequences for biocontrol

Self-superparasitism may not be a desirable characteristic when it occurs in a biocontrol agent. When host density is low, females may respond by increasing clutch sizes and/or increasing chances of accepting previously parasitised hosts. The time taken to oviposit is likely to be less than the time taken to find additional hosts, particularly if hosts are rare. Thus, pest species survive below a certain density threshold, which may be above a targeted economically sustainable level. Similarly, if self-superparasitism is adopted with rare non-target host species in a native environment, then the parasitoid may be less likely to drive a rare species to extinction by parasitising all available individuals. The search for low density hosts in distantly spaced patches may be abandoned at a particular egg or lifetime stage in favour of superparasitism of previously located hosts.

Conclusion

The present study indicates that *T. brevifacies* superparasitism occurs in the field when hosts are rare. This may pose some disadvantages to the effectiveness of a parasitoid biocontrol agent but could prove advantageous for the survival of rare non-target hosts. Superparasitism is adaptive at low host densities given the costs of this strategy measured in the present study. Indirect costs of superparasitism were not measured in this study but could limit the fitness of small progeny.

REFERENCES

Adamo, S.A., Robert, D., Perez, J., Hoy, R.R. (1995) The response of an insect parasitoid *Ormia ochracea* (Tachinidae), to the uncertainty of larval success during infestation. *Behaviour Ecology and Sociobiology* **36**: 111-118.

Askew, R.R. (1971) Parasitic Insects. Heinmann Educational Books Ltd., London, U.K.

Belshaw, R. (1993) Tachinid Flies: Diptera Tachinidae. Handbook for the identification of British insects. Volume 10 (part 4a). Royal Entomological Society of London.

Collins, M.D., Dixon, A.F.G. (1986) The effect of egg depletion on the foraging behaviour of an aphid parasitoid. *Journal of Applied Entomology* **102**: 342-352.

Early, J. W. (1984) Parasites and Predators. In: *New Zealand Pest and Beneficial Insects*. Scott, R.R. (Ed) pp 271-308. Lincoln University of Agriculture, Canterbury, New Zealand.

Fisher, R.A. (1930) The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Godfray, H.J.C. (1987) The evolution of clutch size in parasitic wasps. *American Naturalist* **129**: 221-233.

Godfray, H.J.C. (1994) Parasitoids, behavioural and evolutionary ecology. Princeton University Press, New Jersey, USA.

Hardy, I.C.W., Griffiths, N.T., Godfray, H.C.J. (1992) Clutch size in a parasitoid wasp: a manipulation experiment. *Journal of Animal Ecology* **61**: 121-129.

Herrebout, W. (1969) Some aspects of host selection in *Eucarcelia rutilla* (Diptera: Tachinidae). *Netherlands Journal of Zoology* **58**: 340-355.

Hubbard, S.F., Marriss, G., Reynolds, A., Rowe, G.W. (1987) Adaptive patterns in the avoidance of superparasitism by solitary parasitic wasps. *Journal of Animal Ecology* **56**: 387-401.

Lack, D. (1947) The significance of clutch size. *Ibis* **89**: 309-352.

Moratorio, M.S. (1987) Effect of host species on the parasitoids *Anagrus mutans* and *Anagrus silwoodenis* Walker (Hymenoptera: Mymaridae). *Environmental Entomology* **16:** 825-827.

Petersen, G.H.I. (1996) The importance of being larger: parasitoid intruder-owner contests and their implications for clutch size. *Animal Behaviour* **51**: 1364-1373

Singh, P., (1983) A general purpose laboratory diet mixture for rearing insects. *Insect Science and its Application* **4**: 357-362.

Speirs, D.C., Sherratt, T.N., Hubbard, S.F. (1991) Parasitoid diets: does superparasitism pay ? *Trends in Evolution and Ecology* **6**:22-25.

Takasu, K., Hirose, Y. (1991) The parasitoid *Ooencyrtus nezarae* (Hymenoptera: Encyrtidae) prefers hosts parasitised by conspecifics over unparasitised hosts. *Oecologia* **87**: 319-323.

Thomas, W. P. (1975) Additional notes on leafroller. *The New Zealand Orchardist*, Nov: 354-355.

van Alphen, J.J.M., Nell, H.W. (1982) Superparasitism and host discrimination by *Asobara tabida* (Braconidae: Alysiinae) larval parasitoid of Drosophilidae. *Netherlands Journal of Zoology* **32**: 232-60.

van Alphen, J.J.M., Visser, M.E. (1990) Superparasitism as an adaptive strategy for insect parasitoids. *Annual Review of Entomology* **35**: 59-79.

van Baaron, J., Boivin, G., Nenon, J.P. (1995) Intraspecific hyperparasitism in a primary hymenopteran parasitoid. *Behavioural Ecology and Sociobiology* **36**: 237-242.

Visser, M.E., Luyckx, B., Nell, H.W., Boskamp, G.J.F. (1992) Adaptive superparasitism in solitary parasitoids: marking of parasitized hosts in relation to the pay-off from superparasitism. *Ecological Entomology* **17**: 75-82.

Volkl, W., Mackauer, M. (1990) Age-specific host discrimination by the aphid parasitoid *Ephedrus californicus* (Hymenoptera: Aphidiidae). *Canadian Entomologist* **122**: 349-361.

Waage, J.K., Ng, S.M. (1984) The reproductive strategy of a parasitic wasp. Optimal progeny allocation in *Trichogramma evanescens*. *Journal of Animal Ecology* **53**: 401-415.

Wearing, C.H., Thomas, W.P., Dugdale, J.S., Danthanarayana, W. (1991) Tortricid pests of pome and stone fruits, Australian and New Zealand species, in *Tortricid Pests, Their Biology, Natural Enemies and Control* (van der Geest, L..P.S. & Evenhuis, H.H., Eds). Elsevier Science Publishers B.V, Amsterdam, The Netherlands. pp 453-472.

Weatherhead, P.J., Robertson, R.J. (1979) Offspring quality and the polygyny threshold: the sexy son hypothesis. *American Naturalist* **113**: 201-208.

Wilkinson, L., Blank, G., Gruber, C. (1996) Desk top data analysis with SYSTAT. Prentice Hall, New Jersey, USA.

Quantifying the distribution of the tachinid parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) and its larval tortricid hosts within forest patches: how invasible are native forest remnants ?

ABSTRACT

The abundance of the tachinid parasitoid *Trigonospila brevifacies* and its tortricid hosts were compared in two height strata levels and between the edge and centre zones of forest patches. Both the parasitoid and its hosts were more abundant in the edge zone of small patches of broadleaf/podocarp forest. A larger scale, multi-site survey of host density and *T. brevifacies* abundance, carried out over two years, was inconclusive as to the relationship between levels of parasitism and host density. *Trigonospila brevifacies* preference for, or limitation to, forest edges may provide non-target native Lepidoptera inhabiting centre forest zones with refuges from parasitism by the tachinid.

INTRODUCTION

Humans inadvertently or purposefully, as in the case of biological control agents, re-distribute species beyond the boundaries of their native ranges. If they successfully establish, these species then invade new habitats (Vitousek *et al.*, 1997). Hengeveld (1989) defines invasions as the entry of a species to a geographical region where it was previously absent. The term invasion is often applied when the invader species has a negative impact on the resident species of an area (Hengeveld 1989).

The Australian tachinid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) was intentionally introduced in conjunction with *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae) to control the pest *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), as it was believed that New Zealand was depauperate in parasitoids of late-instar and pupal host stages (Thomas, 1989). *Trigonospila brevifacies* has since invaded native forests where it attacks eight species of non-target native leafroller species in native habitats (Chapter 3). It has been speculated that *T. brevifacies* may have caused a reduction in the abundance of any non-target native species (Roberts, 1986; Russell, 1986). The existence of host refuges may play a key role in reducing the level of negative impact the parasitoid has

on non-target host species. The determine whether such refuges exist can only be determined by a study of the invasibility of native habitats by *T. brevifacies*, and which areas of these habitats are exploited by the parasitoid.

Not all habitats or zones of habitats may be suitable for colonisation by new species and thus this impact may be dissimilar between habitat types. Availability of food is an important determinant of the distribution of insects within and between habitats (Ross *et al.*, 1982). Parasitoid distribution within habitats has also been associated with host distribution (Waage, 1983) and the spatial arrangement of host habitat (Kruess & Tscharntke, 1994; Roland & Taylor, 1997). The effect a parasitoid has on the population dynamics of a host species can vary depending on whether it's level of parasitism is dependent on host density or whether habitat structure determines parasitoid distribution. It is thought that outbreaks in populations of the forest tent caterpillar (*Malacosoma disstria* Hubner) are curbed in continuous forests because some of it's tachinid parasitoids respond positively to host density (Roland & Taylor, 1997). However, Roland & Taylor (1997) also found outbreaks were more prevalent in fragmented forest as some of the tachinid parasitoids of *M. disstria* were less abundant in fragmented habitats. Because of host density associations or preferences for certain types of habitat, parasitoid species may exploit only some of the potential prey patches within a habitat. Therefore it is possible that *T. brevifacies* only exploits certain microhabitats of the various leafroller species found in New Zealand forests, such that other species or individuals found in other forest strata or microhabitats may escape, or receive lower levels, of parasitism.

The primary aim of this work was to determine how invasible native forest patches are to *T. brevifacies* and which zones or strata are exploited by it, by comparing the distribution of native Tortricidae within forest patches to that of *T. brevifacies* and providing an indication of parasitism risk between the edge and centre of patches. Data from a two-year, four-site survey comparing host density and levels of parasitism are used to determine if *T. brevifacies* rate of parasitism is dependent on host density. These data are discussed in relation to whether *T. brevifacies* abundance is linked to certain habitat zones irrespective of host density or whether distribution of the parasitoid follows that of its host species.

METHODS

Laboratory experiments

A reliable method of asse sing the presence or absence of *T. brevifacies* from strata and zones in a variety of vegetation ypes was developed. Although adult *T. brevifacies* have previously been collected in malaise t ap samples (J.S. Dugdale, unpub. data), trials with this method yielded few specimens fro a dense forest patches in the Bay of Plenty where *T. brevifacies* was frequently observed.

Yellow sticky trap have been used successfully to trap Tachinidae species (Burk, 1982; Raspi, 1982) and ar reported to be a successful method for comparing population abundances spatially and te porally (Weseloh, 1981;), hence this method was chosen for trial to test its effectiveness at tr pping *T. brevifacies*. Coll and Bottrell (1996) speculated that yellow panel traps may cha ge the appearance of a habitat to some parasitoid species in cropping situations thus bia g results by their attractant ability. In the present study, it seems likely that yellow sticky trap will only attract tachinids from the trap vicinity given the structural complexity of bro leaf/podocarp forests. Preliminary field trials indicated that *T. brevifacies* could be caught o yellow and blue sticky traps. However, further experiments under controlled conditions w re required to determine which colour trap was most attractive to *T. brevifacies* and whether ale and female *T. brevifacies* were trapped differentially by this method.

Sheets of coloured co gated plastic card were cut into 20 cm x 20 cm squares and a commercially available insect t p adhesive (TacTrap™) applied. Blue, yellow and clear plastic cards were trialed in the labora ry to test their attractiveness to *T. brevifacies*. Cards were attached vertically to the labora ry walls. Each group of three cards were placed side-by-side and 20 cm apart. The four grou s of three cards were spaced 2 m apart. Each replicate group contained a clear, a blue and a y low card. Cards were placed in random order within each replicate. Fifteen female and 15 r ale *T. brevifacies* were periodically released over a one hour period into the laboratory (10 m l 4 m floor space). The cards were removed after 12 hours and the number and gender of flie caught on each trap were noted. This experiment was repeated on two further occasions

Field sampling of host and parasitoid distribution in forest patches

Sites

Two replicate sites of broadleaf/podocarp native forest remnant were chosen at Tane (175° 52'E, 40° 70'S), in the northern Wairarapa. The sites were of similar age (100 year old secondary growth forest), elevation, aspect, and size (approximately 4 hectares). Sites were inspected to ensure that *T. brevifacies* was present.

Parasitoid sampling

Two, two-week long sampling periods were carried out in February and March 1998 to determine the abundance of *T. brevifacies* in two height strata and in the edge and centre of the forest patches. These sampling occasions were timed to trap different generations of *T. brevifacies*. Twenty yellow sticky traps were placed at each height (1 m and 3 m above ground level), on trees closest to 10 m intervals on each of two 200 m transects along the forest edge and repeated two 200 m transects at the forest centre, approximately 50 m from the edge at both sites. A total of 80 traps were placed at each site on each sampling occasion. The tree species, aspect of traps on each tree, the trap height, and the number and gender of *T. brevifacies* trapped during each sampling period were recorded.

Host sampling

The same forest patches, were used to survey the distribution of larval host Tortricidae. Twelve trees were sampled at 10 m intervals along a 120 m transect at the edge of each forest patch. Density counts of Tortricidae were made by counting larvae within 3 m x 3 m quadrats at two strata levels, (approximately 2 m and 5 m above ground) level for each tree. Samples were taken while standing in a tractor loader bucket. The bucket width (1.5 m) and a tape measure were used to define a quadrat area of 3 m^2. Tortricid larvae were counted at each height within a tree canopy from one aspect and repeated from a second aspect for each tree sampled.

It was not practicable to use the loader bucket method in the centre of the forest patches. Instead, 12 trees or shrubs were randomly chosen at the centre of each site and tortricid larvae counted separately on each tree, as above, at heights of 1 m and 2 m above ground level.

Two-year survey of host density and levels of parasitism

At sites in the Bay of Plenty, Manawatu and Wairarapa seasonal samples of tortricid larvae were collected to determine the levels of *T. brevifacies* parasitism in different seasons and

locations over a two year period. Insect host density is frequently estimated by setting an arbitrary collection time and measuring the number of individuals collected within that sampling period. A disadvantage of this method is that sampling error becomes unstable and a more stable sampling error is achieved with a balanced design. So, 40 caterpillars were collected during each sampling occasion from each site and the time taken to collect these samples gave an estimate of host density. Host density was then calculated as 40 divided by the collection time per sampling occasion, giving a value for the mean number of caterpillars collected per minute. Sites and sampling procedure are described in Chapters 3 and 5.

Data analysis

The selectivity by male and female *T. brevifacies* for blue, clear or yellow sticky traps in the laboratory was tested by a 1-way Chi-square test.

Associations between sticky trap height (1 m or 3 m) and location (forest edge or centre) and the frequency at which *T. brevifacies* were trapped at each forest patch was initially explored using two-way Chi-square tables. A log-linear model was then used to test for interactions between trap height and edge or centre effects on the success rate (number of flies caught) of individual traps. Trap catches of 1 or more flies were analysed for associations between the gender of trapped parasitoids, trap height and trap location (edge/centre) using two-way Chi-square tests.

To test whether the density of host larvae differed between sites, tree species, aspect, trap height and edge/centre, an Analysis of Variance of was carried out in SYSTAT (Wilkinson *et al.*, 1996). The experimental design was initially balanced with respect to site, edge/centre zone and height. However, preliminary analysis suggested that larval density differed significantly between the 12 tree species sampled (Fig. 1). As tree species could confound height and edge/centre patterns of larval host density, the analysis was limited to the two most common tree species, tawa (*Beilschmiedia tawa* A. Cunn.) and mahoe (*Melicytus ramiflorus* Forster), found at both sites and zones. The data were still unbalanced with respect to combinations of aspect and tree species.

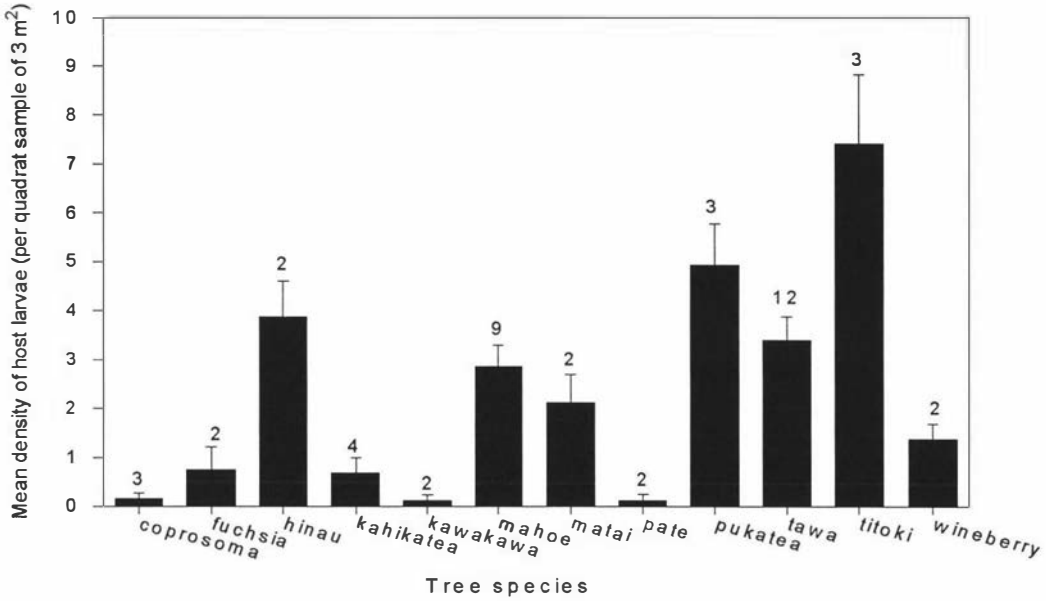


Figure 1. Density of tortricid host larvae on native tree species. Error bars represent standard error values and numbers above the bars represent the number of trees of each species sampled. The two most abundant tree species were used for later analysis.

The relationship between *T. brevifacies* parasitism and host density was analysed using data from seven sampling occasions over two years, at four sites. Data were analysed using a logistic regression in SYSTAT 8. A full model with all interaction terms present could not be fitted because of problems with colinearity, perhaps due to the method of calculating host density. Parasitism was the dependent variable used, with site, season, and host density as independent variables. The main effects (season and region) were tested for interactions.

RESULTS

Laboratory experiments

The frequencies with which *T. brevifacies* were trapped on yellow, blue and clear sticky traps were significantly different ($\chi^2_2 = 64.47$, $P=0.001$). Yellow was the colour most preferred, capturing 94.7 % of flies trapped. The frequencies at which male and females *T. brevifacies* were trapped on yellow sticky traps were not significantly different ($\chi^2_2 = 2.01$, $P=0.365$). Yellow sticky traps were chosen to measure *T. brevifacies* abundance in the field.

Field experiments

Host distribution

A survey was conducted to determine whether the distribution of larval Tortricidae, predominant hosts of *T. brevifacies*, exhibited a similar pattern to the parasitoids distribution in forest patches. Because of the unbalanced design the data, host distribution analysis was limited to larvae on the two most common tree species surveyed. A multi-way ANOVA of the four independent variables (aspect, sample height, edge/centre zones and site) measured indicated that larval density was not significantly different between mahoe and tawa trees (F_1 =0.08, P=0.775), that caterpillar density was greater at the lower level sampled (approximately 2 m above ground level) (F_1 =5.06, P=0.027), that the density of larval hosts was greater on the edge zones of forest patches than at the centre zones (F_1 =84.2, P<0.005), that larval density did not vary with the aspect at which samples were taken (F_1 =0.002, P=0.963), and that sites were not significantly different (F_1 =3.57, P=0.062). In conclusion, host larvae in both sites were found to occur at higher densities and in the lower canopy at the edge of forest patches (Fig. 2).

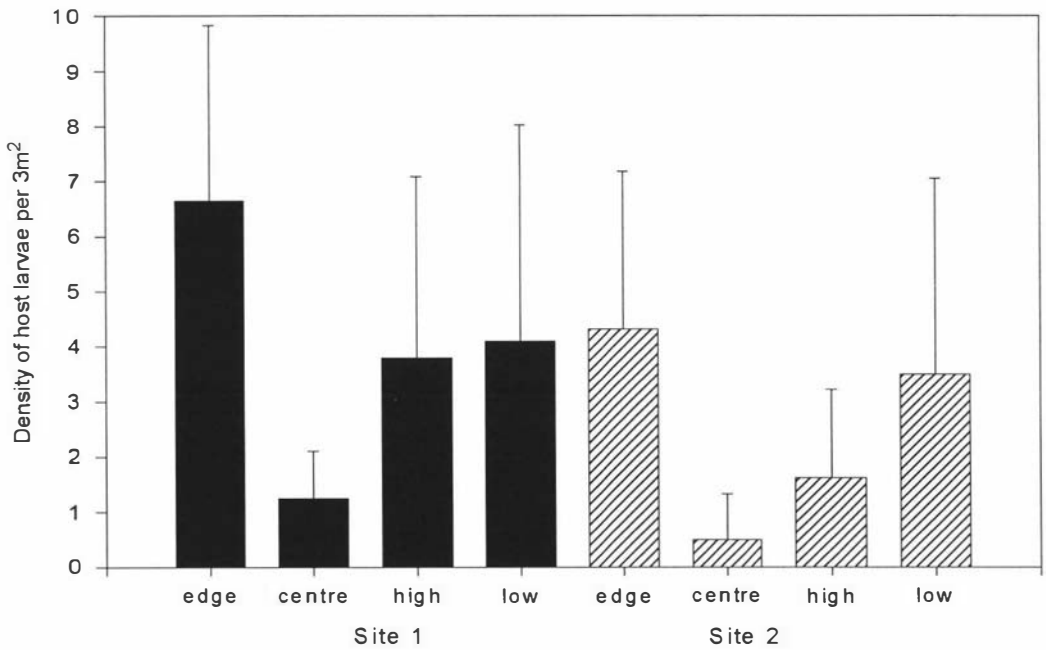


Figure 2. Comparison of host caterpillar density between forest patches at the edge and centre zones and between high and low samples. Error bars represent standard error values.

Ten 2-way interaction terms combining five independent variable categories (tree species, aspect, sample height, site, edge/centre zones) were also tested for significance. Only the edge/centre and sample height interaction term produced a significant interaction (F_1 =6.71, P<0.05). Although larval host densities at the edge were six times greater than those found in the centre zones, the greatest difference in larval densities between edge and centre occurred at low sample heights (Table 1).

Table 1. Mean host larval density (individuals per 3 m^2) at edge and centre zones and at high and low strata. Data are combined for sites 1 and 2.

	centre zone	edge zone
high samples	0.89 (SE: ± 0.217)	4.2 (SE: ± 0.580)
low samples	0.73 (SE: ± 0.190)	6.3 (SE: ± 0.659)

Parasitoid distribution

Approximately 20 % of the yellow sticky traps caught flies in the field. The frequency with which *T. brevifacies* adults were trapped was not significantly different between the two sites (χ^2_1 = 0.26, P=0.605). Edge traps captured twice as many flies as centre traps (χ^2_1 = 8.57, P<0.005). While 72 % of flies caught in the centre were captured on low traps, catch rates between low and high traps were not significantly different when edge and centre catches were combined (χ^2_1 = 1.68, P=0.195) (Fig. 3).

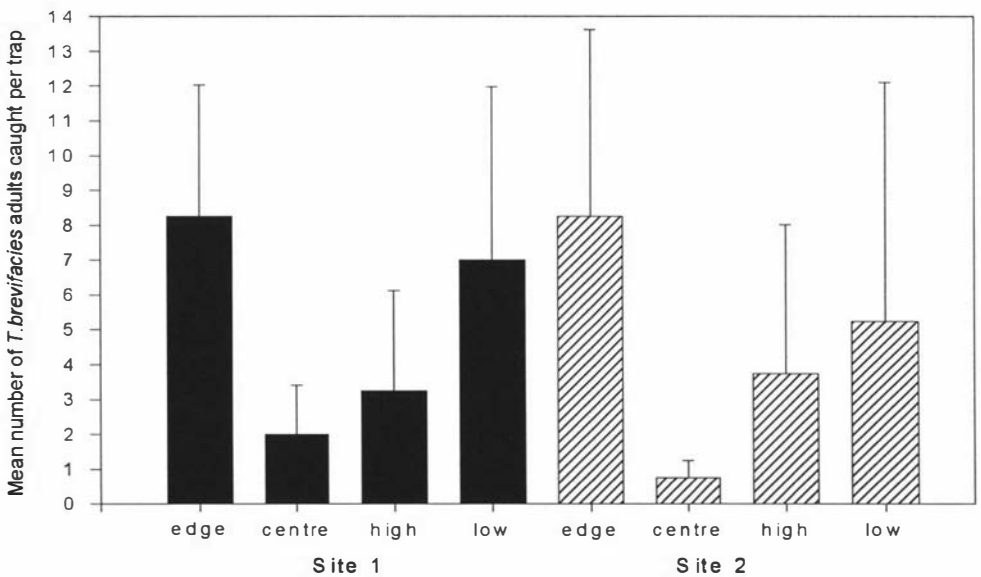


Figure 3. Distribution of *T. brevifacies* adults within forest patches determined by sticky trap sampling. Error bars represent standard error values.

Centre-zone low traps captured flies at a rate of 2.7 times greater than that of high traps, while low edge-zone traps captured 1.5 times more flies than high traps. A log-linear model used to test for 3-way interactions between trap height, trap location and capture rate indicated that there was no significant interaction between the rate at which low traps captured flies between the edge and centre zones of forest patches ($\chi^2_2 = 1.70$, P=0.428). A significant interaction was detected between the frequency with which flies were captured at the centre- and edge-zones of the forest ($\chi^2_1 = 4.02$, P=0.0449), as edge traps were more successful. However, there was no significant interaction between high and low traps and the numbers of flies captured ($\chi^2_1 = 1.68$, P=0.195).

There was no significant difference in the frequency at which female and male flies were caught on high and low traps ($\chi^2_1 = 0.12$, P=0.725). Both male and female flies were more frequently captured on 1 m high traps than on 3 m traps, with approximately 60% of both males and females captured at the lower trap level. No significant difference was found between the frequency with which each gender was captured in the edge and centre zones ($\chi^2_1 = 2.60$, P=0.107). Both male (80.4 %) and female (93.5 %) *T. brevifacies* were more frequently captured on the edge zone.

Relationship between levels of parasitism and host density

The relationship between *T. brevifacies* parasitism and host density is not simple when multi-season and multi-site data are combined. Low host density (0.2 larvae collected per minute) was associated with high levels of parasitism. Intermediate host densities (0.3 larvae collected per minute) appear to have the lowest rates of parasitism, while parasitism levels increase at higher host densities (0.6 larvae collected per minute) (Figure 4).

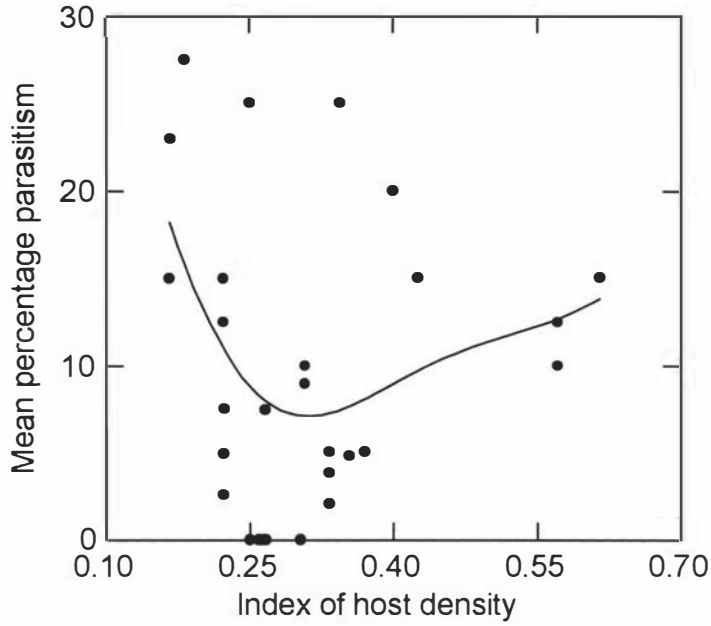


Figure 4. Trends in *T. brevifacies* parasitism at North Island native forest sites between 1996 and 1998 in relation to host density. Percentage parasitism and host density values represent seasonal averages at the four forest sites. The index of host density represents the number of larvae collected per minute. Smoother applied to line is a DWLS.

Results for the logistic regression analysis of levels of parasitism are presented in Table 2. Tortricid host density by itself, was not significantly associated with *T. brevifacies* parasitism (χ^2_1 =.0215, P=0.887) (also see Figure 4). Levels of parasitism were not significantly different in the two regions (χ^2_1 =1.250, P=0.259). However, there were significant differences in parasitism levels among the seven sampling seasons (χ^2_6 =36.445, P<0.0000). Estimated odds ratios, indicated the probability of parasitism was significantly higher in autumn 1997 (mean parasitism 14.75 ± 3.66%), autumn 1998 (mean parasitism 13.2 ± 4.49%) and summer 1996 (13.75 ± 4.84%) and low in spring 1997 (mean parasitism 1.2 ± 1.21%).

When season and host density were combined in the model, density was found to have a marginally significant effect on host density (χ^2_1 =3.711, P=0.0541). However, the association between parasitism and host density became significant when both regional and seasonal variables were included in the model (χ^2_1 =5.839, P=0.0157). The odds ratio for the density effect (0.085) was less than one, indicating that as host density increased the probability

of parasitism declined. Though much of the relationship between parasitism rate and host density could be due to seasonal changes in host density and parasitoid activity.

Most attempts to fit logistic models with interaction terms failed to converge. The exception was the two-way interaction between season and region which was significant (χ^2_6 =23.313, P=0.0007). However, since host density was almost completely specified by the combination of region and season, density was no longer significant. This would also be the reason for the lack of convergence of models with other interactions. Because of the limited replication in this study and inability to experimentally control host density, it is not possible to determine whether a host density effect on parasitism really exists or whether it could be due to complex seasonal and regional variation in the levels of parasitism.

Table 2. Logistic regression models of *Trigonospila brevifacies* parasitism levels.

Model	Indep. variable	log likelihood	tested against	df	Chi-square	P value
0	constant only	-359.26	-	-	-	-
1	density	-359.25	0	1	.0215	0.8871
2	region	-358.63	0	1	1.250	0.2597
3	season	-341.03	0	6	36.445	0.0000
4	season+density	-339.18	3	1	3.711	0.0541
5	season+region	-340.40	3	1	1.258	0.2620
6	region+season +density	-337.48	5	1	5.839	0.0157
7	Two-way interaction model 6 + region*season	-325.83	6	6	23.313	0.0007

DISCUSSION

Distribution of host Lepidoptera within forest patches

Tortricid host density in the broadleaf/podocarp forest patches sampled was greatest at the edge zone and may have been related to patch quality. For example, preferred host plant species or the nutritional quality of host plants. Edge zone plants receive more direct sunlight than plants in the lower strata of forest centres. Higher light levels promote higher levels of photosynthesis and new growth, providing a higher quality food source for herbivorous insects (Ross *et al.*, 1982). Analysis of plant sugar levels would be required to test whether tortricid larval density is related to plant quality and whether plant quality differs between the edge and centre of broadleaf/podocarp forest zones. Alternatively, the high density of hosts at the forest edge may be due to the invasion of Tortricidae from the surrounding habitat. Invasions of orchards by tortricids from vegetation reservoirs such as shelter belts and native forest have been demonstrated in biological control literature (Thomas, 1989).

Distribution of adult *T. brevifacies* within forest patches

Trigonospila brevifacies was more abundant at the edge and at lower strata levels of the forest patches sampled. Males and females were captured at similar frequencies in the two forest zones and strata, and both were least abundant on high traps in the centre zone.

Traps on most trees caught similar numbers of flies except for those on pukatea (*Laurelia novae-zealandiae* A. Cunn.), which caught between 1.4 and 2 times more flies than traps placed on other tree species. Different tree species predominated at the edge and centre of the sites it is impossible to control for this in field experiments.

Although male and female *T. brevifacies* were both more abundant along the edge zone of forest patches, they may exploit this zone for different purposes. The distribution of female *T. brevifacies* was of a similar pattern to the distribution of larval hosts. Both parasitoids and hosts were more abundant along the edge of forest zones and female parasitoids appeared to be aggregating in areas of highest host density. Roland and Taylor (1997) found that three tachinid parasitoid species of the forest tent caterpillar (*M. disstria*) caused higher levels of parasitism in areas of high host density. A fourth tachinid, *Carcelia malacosomae,* exerted higher levels of parasitism in fragmented forest or the edges of continuous forest. However, when *M. disstria* occurred at high density in continuous forest this parasitoid was found not to exploit these prey patches.

Forest structure was thought to impede movement by *C. malacosomae* through forests and so limit its impact on high density prey patches that occur there (Roland & Taylor, 1997). *Trigonospila brevifacies* was similarly more abundant along forest edges and exerted greater levels of parasitism in this forest zone (Chapter 7). Whether *T. brevifacies* movement is similarly limited by forest structure or whether the tachinid is aggregating in areas of high host abundance is as yet unclear.

Parker (1978) stated that male insect distribution is dependent on finding patches with females in habitats of discontinuously distributed resources. Calypterate Diptera are known to "sunspot", in which leks are formed in sunlit areas from where males can intercept passing females or disperse intruder males. These leks are not necessarily resource-based (Parker, 1978). Male *T. brevifacies* were frequently observed forming leks of 3-4 individuals, spaced approximately 50 cm apart, on vegetation receiving direct sunlight on forest edges (V.Munro, unpub. data). Thus, males may be more abundant along forest edge zones as this is the best location to attract mates while female distribution could be dependent on host abundance in these areas.

Location of hosts most at risk of parasitism in forest patches

The similar patterns of distribution for hosts and parasitoids in forest patches has important consequences for the impact of *T. brevifacies* on non-target hosts. When parasitoids aggregate in some patches of a habitat, other patches where parasitoid density is low may become host refuges (Godfray, 1994). Parasitoid distribution is not always determined by host density. Habitat structure may also be important in determining the distribution of some parasitoid species (Roland & Taylor, 1997). The data from the present study indicated that *T. brevifacies* is most abundant where its primary host group, larval Tortricidae, occur at higher densities. The caterpillar population that occurred in the centre forest zone were exposed to 6 times fewer parasitoids than populations on the edge of forest patches. But the ratio of the (density indices) hosts to parasitoids was consistently 1.5 - 2 times whether hosts occurred on the edge or the centre of forests. This implies that lepidopteran species that are more abundant at patch centres could obtain some refuge from *T. brevifacies* parasitism. Similarly if tortricids increase in abundance in some seasons at forest centres (e.g., due to microclimate changes in forest centres during summer) and *T. brevifacies* abundance does not increase correspondingly (e.g.,

because habitat structure prevents colonisation of centres), then again under these conditions forest centres may provide refuge to some of the host population.

Relationship between levels of parasitism and host density

Data from the two-year survey showed a statistical association between the density of host Tortricidae and levels of *T. brevifacies* parasitism after adjusting for seasonal and regional effects. These results suggest that at the spatial scale of forest patches and the temporal scale of seasonal sampling (with no samples taken in winter) the probability of parasitism declined as host density increased. However, whether this relationship is causal or not is unclear. The lack of differentiation between edge and centre rates of parasitism when sampling may also have complicated this result.

Season had the largest effect on percentage parasitism, however none of the model variables (season, region, host density) explained much of the variance in parasitism levels. For the most complex model that could be fitted, the rho-square value was only 0.093.

If the patterns of host density and levels of *T. brevifacies* parasitism in Figure 4 are real phenomena what could account for these patterns ? 1).When low host density was associated with high parasitism levels, parasitoid searching may have been efficient and a large proportion of hosts were found. 2) When medium host densities were associated with low levels of *T. brevifacies* parasitism, the parasitoids life cycle may have been out of synchrony with that of its hosts. 3) High host densities associated with high levels of parasitism, may result from dispersal by *T. brevifacies* to areas of high host density. 4) Or parasitism and host density may not be causally linked, the observed patterns could be an artifact of season impacting on other environmental variables, which differentially affect host and parasitoid populations.

In conclusion, the lower density of *T. brevifacies* in the centre of forest patches could be due to a habitat constraint limiting movement into the forest, or it could be a direct response to host density. If the former, forest centres could be refuges for caterpillars from attack by *T. brevifacies*. If the latter, then forest centres would only be apparent refuges as the low density of caterpillar population could still be exposed to the same rate of parasitism. Experimental manipulation of caterpillar densities in centres and edges of forest patches, or measurements of parasitism rates at smaller spatial scales are needed to distinguish between these two outcomes.

REFERENCES

Burk, T. (1982) Sticky panel catches of the tachinid *Euphasiopteryx ochracea*. *Florida Entomologist* **65**: 291-292.

Coll, M., Bottrell, D.G. (1996) Movement of an insect parasitoid in simple and diverse plant assemblages. *Ecological Entomology* **21**: 141-149.

Godfray, H.J.C. (1994) Parasitoids, behavioural and evolutionary ecology. Princeton University Press, New Jersey, USA.

Hengeveld, R. (1989) Biological Invasions. Chapman and Hall, London, UK.

Kruess, A., Tscharntke, T. (1994) Habitat fragmentation, species loss and biological control. *Science* **264**: 1581-1584.

Munro, V.M.W. (1998) A record of the releases and recoveries of the Australian parasitoids *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) introduced to New Zealand for leafroller control. *New Zealand Entomologist* **21**: 81-91.

Parker, G.A. (1978) Evolution of competitive mate searching. *Annual Review of Entomology* **23**: 173-196.

Raspi, A. (1982) Considerazioni preliminari sulla cattura di entomofauna utile mediante L'Impiego di trappole chemiochromotropiche nell 'oliveto. *Frustula-Entomologica* **5**: 103-109.

Roberts, L.I.N. (1986) The practice of biological control - implications for conservation, science and community. *Weta* **9**:76-84.

Roland, J., Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**: 710-713.

Ross, H.H., Ross, C.A., Ross, J.R.P. (1982) A Textbook of Entomology. John Wiley and Sons, New York, U.S.A.

Russell, D.A. (1986) The role of the entomological society in insect conservation in New Zealand. *Weta* **9**: 44-54.

Thomas, W.P. (1989) *Epiphyas postvittana*, the lightbrown apple moth, in *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987* (Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P., Eds). CAB International, Wallingford, U.K. pp 187-195.

Vitousek, P. M., D'Antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R. (1997) Introduced species: A significant component of human-caused global change. *New Zealand Entomologist* **21**: 1-16.

Waage, J.K. (1983) Aggregation of field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera: Ichneumonidae). *Ecological Entomology* **8**: 447-453.

Weseloh, R.M. (1981) Relationship between coloured sticky panel catches and reproductive behavior of forest tachinid parasitoids. *Environmental Entomology* **10**: 131-135.

Wilkinson, L., Blank, G., Gruber, C. (1996) Desk top data analysis with SYSTAT. Prentice Hall, New Jersey, USA.

Existence of refuges for the non-target hosts of *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) within native forest patches.

ABSTRACT

Both host density and habitat structure can affect the distribution of parasitoids and so the level of parasitism occurring within and between habitats. Differences in the level of parasitism by a tachinid species within forest zones were investigated. Parasitism by the multivoltine parasitoid *Trigonospila brevifacies* (Diptera: Tachinidae) was estimated by placing trap hosts in the field to coincide with two generations of *Ctenopseustis obliquana* (Lepidoptera: Tortricidae). The mean level of parasitism across the sites and generations in a season was 8.5 %. The level of parasitism was 30 % at forest edges and declined steeply to nearly zero at 30 m into the forest. This demonstrates the existence of host refuges in forest centres.

INTRODUCTION

Increasingly the issue of the non-target effects of biocontrol agents on non-target species is being considered (Howarth, 1991; Simberloff & Stiling, 1996; Sands, 1997; Barratt *et al.*, in press). The type of habitat preferred by natural enemies and their spatial distribution within habitats, are factors which determine both whether biocontrol agents will successfully control target pests and whether the entomophage is likely to invade the habitats of non-target hosts and attack them (Philogene, 1998; Hopper, 1998).

Percentage parasitism is a useful representation of the impact a parasitoid is having on a host population at a specific time if recruitment, susceptible host life stage and host density are determined (van Driesche *et al.*, 1991). Habitat structure is one factor that can limit parasitoid distribution and the level of parasitism occurring in different areas (Marino & Landis, 1996).

Roland & Taylor's (1997) study of tachinid parasitoids of the forest tent caterpillar, *Malacosoma disstria* Hubner (Lasiocampidae), demonstrated the influence of habitat structure on host-parasitoid population dynamics. Some species of tachinid concentrated their parasitism on hosts in fragmented forests and edge zones of forests, while others were apparently limited to continuous forest habitats (Roland & Taylor, 1997). Therefore, the level of parasitism

exerted by parasitoid species may vary between zones within a forest and between forests of different structural configurations.

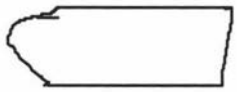
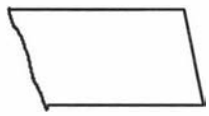
New Zealand native forests have become increasingly fragmented by land-clearances for agricultural purposes in the last 150 years (Young & Mitchell, 1994). The introduced biological control agent *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) has invaded native forests in New Zealand (Munro, 1998a, Munro, 1998b). Whether *T. brevifacies* is limited by certain forest structural complexity and whether this affects its impact on non-target Lepidoptera is unknown. The first aim of this work was to determine the level of parasitism exerted by *T. brevifacies* on a non-target host, *Ctenopseustis obliquana* (Walker) (Lepidoptera: Tortricidae), in native habitats. This species is frequently parasitised by *T. brevifacies* in native forests (Chapter 3). The risk of parasitism to non-target host species posed by *T. brevifacies* may vary depending on a host's location in a forest patch. Patterns of parasitism on trap hosts placed on transects from edge to centre in three forests were used to test this hypothesis. A logistic regression model was used to estimate the probability of *T. brevifacies* parasitism for hosts along a gradient from edge to centre within forest patches and to determine if host refuges could exist.

METHODS

Sites

The experiment was carried out in three broadleaf/podocarp forest remnants in the Manawatu and Wairarapa regions of the North Island, New Zealand. All sites were of similar structure (mature forest with some history of felling and domestic animal grazing), species composition (broadleaf/podocarp forest), size (4-8 hectares) and situation (forest remnants surrounded by pasture), altitude (50-100 m a.s.l.) and shape (sub-rectangular). Previous surveys had shown that *T. brevifacies* was present at all three sites.

Table 1. Site characteristics.

Site	Location	Size (ha)	Shape
Tane	(175° 52'E, 40° 70'S)	4	
Porewa	(175° 28' E, 40° 2'S)	4	
Koebles	(175° 35' E, 40° 23'S)	8	

Estimation of parasitism levels

The experiment was timed to coincide with the occurrence of late-instar *C. obliquana* in the wild population. Pheromone traps were used to determine when adult emergence was occurring. Host life span has been estimated by D.J. Rogers (Insect Rearing Group, Hort Research, pers. comm.) as approximately 30 days at 18°C under laboratory conditions. This was used to predict the time taken to reach the late-instar larval stage in the field.

Trap hosts are defined as a known number of individuals of a host species, placed in a habitat to measure the timing and level of parasitism. The advantages of using traps hosts over rearing larval hosts collected from a field population are that hosts can be systematically placed in a habitat to provide a balanced experimental design for testing specific hypothesises. Trap hosts also give more precise information of the timing and level and location of parasitism (Van Driesche, 1983).

At each site, trap hosts were established on twelve 50 m transects (3 transects per compass aspect), starting from 5 m outside the forest edge to the interior. A small hole was made in the lid of water-filled plastic containers and 50 cm long branches of mahoe (*Melicytus ramiflorus* Forster) were inserted. On each branch, two leaves were pinned together to form a leafshelter into which one late-instar *C. obliquana* larva was placed. Within a few minutes of placement, most larvae began to web together the leaves of the shelters. A branch with its caterpillar was placed at 5 m increments along the transects. Each of the twelve transects had ten trap hosts, giving a total of 120 trap hosts per site.

At the end of a four-day period all remaining larvae were collected from the mahoe branches and placed in vials with artificial diet. Parasitism of caterpillars by *T. brevifacies* was confirmed by rearing. The experiment was conducted in late January 1998 and repeated in March 1998 during the late-instar stage of the next generation of *C. obliquana*.

Data analysis

Logistic regression was used to determine the risk of parasitism for trap hosts dependent on the distance of host larvae from the patch edge, aspect location and sampling occasion (SYSTAT, Version 8.0). The significance of these affects was determined by Chi-square tests of the log-likelihood ratio.

RESULTS

The levels of parasitism by *T. brevifacies* on trap hosts at the three study sites, Tane, Keebles and Porewa, were not significantly different ($\chi^2_2 = 4.264$, $P=0.119$) and the mean level did not differ between the summer and autumn samples ($\chi^2_1 = 0.56$, $P=0.597$). The overall average level of parasitism on *C. obliquana* trap hosts was 8.5 ± 1.06 % across the three sites. However, parasitism levels were significantly affected by trap host distance from the forest edge ($\chi^2_1 = 115.14$, $P<0.001$). There were no significant interactions between the main effects (site, sampling occasion and distance from the forest edge) (simultaneous test of all interactions $\chi^2_7 = 5.312$, $P=0.879$). Results for the logistic regression analysis are presented in Table 2.

Table 2. Logistic regression models of *Trigonospila brevifacies* parasitism levels at different distances from the forest edge.

Model	Indep. variable	log likelihood	tested against	df	Chi-square	P value
0	constant only	-196.164	-	-	-	-
1	distance	-138.593	0	1	115.142	< 0.00001
2	distance + site	-136.461	1	3	4.264 (df= 2)	0.119
3	distance + site + season	-136.181	2	4	.56 (df=1)	0.454
4	+ two-way interactions	-134.076	3	9	4.210 (df=5)	0.519
5	+ three-way interactions	-133.525	4	11	1.102 (df=2)	0.576
6	all interactions v main effects		3	-	5.312 (df=7)	0.622

Risk of parasitism dependent on location of hosts in forest patches

The logistic regression model was used to determine whether all hosts in a forest patch were subject to the same intensity of parasitism from *T. brevifacies*. The logistic regression model predicted that the average level of parasitism 5 m outside the forest boundary was 40 % and on the forest boundary it was 30 %. The probability of parasitism declines steeply to 5 % for hosts located 12 m from the edge within a forest patch and at 30 m or more from the forest edge *T. brevifacies* parasitism rate is close to zero (Figure 1). Note that at the 40 m point there are five overlapping symbols at zero parasitism in Figure 1.

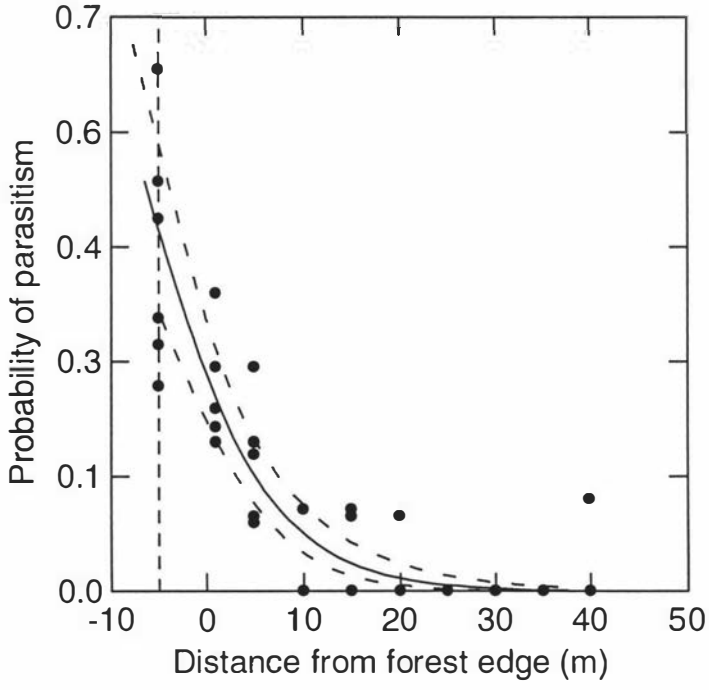


Figure 1. Logistic regression of the risk of parasitism by *T. brevifacies* dependent on host location. Sampling transects started 5 m outside the forest boundary (denoted by the upper limit line) and extended into the forest centre. Dashed lines are 95 % confidence bands.

DISCUSSION

The arrangement of habitat structures may limit parasitoid dispersal, and consequently, patterns of parasitism on hosts. Patterns of natural enemy distribution and parasitism have been linked to both host distribution and the spatial structure of habitats (Waage, 1983; Kruess, & Tscharntke, 1994; Roland & Taylor, 1997). Dispersal of other flying insects is also limited by the structure of habitats. Hedgerows were found to restrict the dispersal of the hoverfly *Melanostoma fasciatum* (Macquart) (Diptera: Syrphidae) between fields (S.Wratten, pers. comm., 1999). The present study determined that host refuges from *T. brevifacies* parasitism exist at the centre of native forest patches.

Host location and the probability of parasitism

Trigonospila brevifacies attacked on average 8 % of the *C. obliquana* trap hosts placed at the three forest sites. However, the overall level of *T. brevifacies* parasitism on non-target hosts may be less significant when determining undesirable impacts on non-target hosts, than the distribution of parasitism through forest patches. A clear distance effect emerged of declining parasitism on trap hosts along transects from forest edges to centres, and this concurs with patterns of adult *T. brevifacies* distribution on sticky traps comparing edge and centre samples in similar forest patches (Chapter 6).

Data modeled in the present study confirm that hosts occurring on forest edges have a significantly higher probability of parasitism by *T. brevifacies*, than hosts located in other forest zones. Therefore, not all non-target hosts within a forest patch are equally exposed to the same level of parasitism, and forest centres provide a host refuge to some individuals of the host population.

Factors influencing *T. brevifacies* distribution

Several factors have been found to determine the patterns of distribution and parasitism observed in tachinid species including host abundance (Roland & Taylor, 1997), limitations on dispersal imposed by the structure of habitats (Roland & Taylor, 1997) and preference of microhabitat and certain types of plant architecture (Weseloh, 1981). Two of these factors appear dominant in determining the distribution of *T. brevifacies* parasitism in forest patches. There is some support for plant architecture and microhabitat determining the distribution of lekking *T. brevifacies* males along forest edges (Chapter 6). However, this is unlikely to limit the distribution of ovipositing females (which live for 30 days) to forest edges once mating has

taken place. The two most likely explanations for the observed patterns of *T. brevifacies* parasitism are response to host density and/or limitations of habitat structure.

Data comparing the distribution of larval tortricid hosts, adult *T. brevifacies* and *T. brevifacies* parasitism within small forest patches shows that parasitoid and host abundances were both higher on forest edges (Chapter 6).

However, the forest edge may also provide conditions preferred by *T. brevifacies* as well as a richer source of hosts. Forest edges in broadleaf/podocarp forests have different microclimates (measured as photosynthetically active radiation, air temperature and vapour pressure deficit) to forest centres (Young & Mitchell, 1994) and a particular microclimate has been demonstrated to be preferred by some parasitoids (Weseloh, 1972). Forest structure may also prevent movement of *T. brevifacies* further into forests. Recently, Roland and Taylor (1997) advanced the hypothesis of habitat structure limiting parasitoid movement when they found evidence of Tachinidae occurring in specific habitat types (fragmented forest and edge zones) with inverse density dependence on host abundance in North American forests.

T. brevifacies distribution and risk to native non-target species

Roberts (1986) speculated that *T. brevifacies* is responsible for a suspected decline in the abundance of *Planotortrix avicenniae* Dugdale (Lepidoptera: Tortricidae) in mangroves around Auckland. The present research suggests that species occupying habitats without continuous canopy, such as *P. avicenniae* in mangrove swamp, may be subject to a more consistent risk of parasitism throughout the population, than the edge-concentrated parasitism of host populations in the broadleaf/podocarp forests.

The mechanism that concentrates *T. brevifacies* parasitism on forest edges may either be in response to host density or habitat structure. Both parasitoids and hosts were more abundant on forest edges. But the ratio of hosts to parasitoids was similar between edges and centres of forests, indicating that higher parasitoid abundance at the forest edge could be related to it's host abundance (Chapter 6). However, when trap hosts were offered for parasitism at a constant density along edge to centre transects at forests in the present study, parasitism was highest at the forest edge. This implies that habitat structure rather than host density may determine where *T. brevifacies* parasitism occurs in forests or that the distribution of the wild host population concentrated *T. brevifacies* parasitism at forest edges in the sites studied.

In conclusion, this work has clarified the implications of *T. brevifacies* for non-target hosts in the native forest habitats it has invaded. *Trigonospila brevifacies* has been shown to parasitise significantly more hosts on forest edges. The model also predicts areas of continuous canopy found within forest patches provide a form of host refuge. Survey data of host and parasitoid distribution patterns indicate that both occurred at higher densities on edge zones in broadleaf/podocarp forests (Chapter 6). This finding also implies that non-target Lepidoptera occurring in habitats with similar habitat structure to edge zones, such as shrubland, have a higher probability of parasitism by *T. brevifacies* across the entire population as the refugia provided by continuous canopy are absent.

REFERENCES

Barratt, B.I.P., Ferguson, C.M., Evans, A.A. (in press) Implications of the effects of introduced biological control agents on native and beneficial non-target species. In: *Balancing Nature: Assessing the Impact of importing Exotic Biological Control Agents - an international perspective* (Purcell, M., Lockwood, J., Howarth, F., Eds). Thomas Say Publication Series.

Godfray, H.J.C. (1994) Parasitoids, behavioural and evolutionary ecology. Princeton University Press, New Jersey, USA.

Howarth, F. G. (1991) Environmental impacts of classical biological control. *Annual Review of Entomology* **36**: 485-509.

Hopper, K.R. (1998) Assessing and improving the safety of introductions for biological control. *Phytoprotection* **79** (suppl.): 84-92.

Kruess, A., Tscharntke, T. (1994) Habitat fragmentation, species loss and biological control. *Science* **264**: 1581-1584.

Marino, P.C, Landis, D.A. (1996) Effects of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecologia et Applicata* **6**: 276-284.

Munro, V.M.W. (1998a) A record of the releases and recoveries of the Australian parasitoids, *Xanthopimpla rhopaloceros* Krieger (Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Tachinidae), introduced to New Zealand for leafroller control. *New Zealand Entomologist* **21**: 81-92.

Munro, V.M.W. (1998b) A retrospective analysis of the establishment and dispersal of the introduced Australian parasitoids *Xanthopimpla rhopaloceros* Krieger (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) within New Zealand. *Biocontrol, Science and Technology* **8**: 559-571.

Philogene, B.J.R. (1998) Research challenges and needs for safe use of arthropods: Introduction. *Phytoprotection* **79** (suppl.): 81-83.

Roberts, L.I.N. (1986) The practice of biological control - implications for conservation, science and community. *The Weta* **9**: 76-84.

Roland, J., Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**: 710-713.

Sands, D.P.A. (1997) The safety of biological control agents: assessing their impact on beneficial and other non-target hosts. *Memoirs of the Museum of Victoria* **56**: 611-615.

Van Driesche, R.G. (1983) Meaning of percent parasitism in studies of insect parasitoids. *Environmental Entomology* **12**:1611-1622.

Van Driesche, R.G., Bellows, T.S., Elkinton, J.S., Gould, J.R., Ferro, D.N. (1991) The meaning of percent parasitism revisited: solutions to the problem of accurately estimating total losses from parasitism. *Environmental Entomology* **20**:1-7.

Waage, J.K. (1983) Aggregation of field parasitoid populations: foraging time allocation by a population of *Diadegma* (Hymenoptera: Ichneumonidae). *Ecological Entomology* **8**: 447-453.

Weseloh, R.M. (1972) Spatial distribution of gypsy moth (Lepidoptera: Lymanidae) and some of its parasitoids within a forest environment. *Entomophaga* **17**: 339-351.

Weseloh, R.M. (1981) Relationship between coloured sticky panel catches and reproductive behavior of forest tachinid parasitoids. *Environmental Entomology* **10**: 131-135.

Young, A., Mitchell, N. (1994) Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* **67**: 63-72.

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Eutorna phaulocosma Meyrick (Lepidoptera: Oecophoridae), a new host for the introduced Australian parasitoid *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae).

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ABSTRACT

Eutorna phaulocosma Meyrick has been identified as a new host of the tachinid parasitoid *Trigonospila brevifacies* (Hardy). *E. phaulocosma* larvae were collected from wild blackberry on a native forest margin and laboratory reared on an artificial diet. *T. brevifacies* larvae emerged from parasitised *E. phaulocosma,* pupated and adult parasitoids emerged 12 days after pupation. The use of *T. brevifacies* as part of an integrated pest management programme for *E. phaulocosma* is discussed.

Keywords: *Trigonospila brevifacies*, *Eutorna phaulocosma*, host record, cane fruit pest, biological control.

INTRODUCTION

Trigonospila brevifacies (Hardy) is a parasitoid of late instar lepidopteran larvae and was introduced to New Zealand in the late 1960s to control the lightbrown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) (Thomas 1989). It is found throughout the North Island (Munro unpublished) in a range of habitats including orchards, urban gardens, exotic forest, farmland and native forest (Munro unpublished), where it has acquired a wide host range. Records to March 1996 indicate that it parasitises 14 species from five families (Oecophoridae, Tortricidae, Pterophoridae, Geometridae and Stathmopodidae). Ten of the 14 hosts are pest species (Green 1984; D. Russell pers.comm. 1996; Wearing 1994). In Australia five species from three families (Tortricidae, Pyralidae and Gelechiidae) (Cantrell 1986; CSIRO unpub. data.) are parasitised.

E. phaulocosma (the blackberry budmoth) is an Australian species accidentally introduced to New Zealand in the 1930s. It can be a minor pest in commercial cane fruit crops, but its damage is limited by the use of insecticide programmes aimed at leafroller

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control (Charles *et al*. 1987). It has colonised wild blackberry and commercially grown *Rubus* species from Auckland to Reefton in the South Island (Charles *et al*. 1987).

This paper records *E. phaulocosma* as a new non-target host of the Australian parasitoid *T. brevifacies*.

METHODS

Lepidopteran larvae were surveyed at a modified native forest site (176° 31'E, 37° 56'S) near the Rotoehu Forest (Bay of Plenty) on the 3 November 1996. Forty larvae were collected. One larva was taken at 2 m intervals along an 80 m transect which extended inwards from the forest edge. The transect included wild blackberry (*Rubus fruticosus*), from which *E. phaulocosma* larvae were collected, on the edge of native forest.

Larvae were transferred from their host vegetation to tubes of general purpose diet (Singh 1983). Specimens were reared in a controlled temperature laboratory (18°C ± 4°C) with a 16 hour photoperiod.

RESULTS AND DISCUSSION

Three *T. brevifacies* larvae pupated beside the remains of newly formed pupal cases of *E. phaulocosma* between 15-16 November. Adult *T. brevifacies* emerged from these puparia on 27 November. The identity of the host Lepidoptera were subsequently confirmed as *E. phaulocosma* (J. S. Dugdale pers.comm. 1996)

The risk posed by *T. brevifacies* to the three native New Zealand *Eutorna* species is unknown. An understanding of the habitat preferences, host finding and ovipositional behaviour of *T. brevifacies* will help assess the level of risk to native *Eutorna* species. However, no native *Eutorna* species are known to occur on Rosaceae (Charles *et al*. 1987) and to date *E. phaulocosma* has only been parasitised by *T. brevifacies* on *Rubus* species of the family Rosaceae.

E. phaulocosma larvae weave silk tubes, drawing in the sides of the leaves of their host plant (Charles *et al*. 1987). This is similar to the behaviour exhibited by tortricid larvae (Penman 1984) which are a common host of *T. brevifacies* (V. Munro unpub. data). Other caterpillar pests of blackberries and boysenberries include *E. postvittana* (Walker), *Planotortrix excessana* (Walker), *Ctenopseustis obliquana* (Walker), *Pyrgotis plagiatana* (Walker), *Heterocrossa adreptella* (Meyrick) (= *Carposina adreptella* Walker), and

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infrequently *Planotortrix notophaea* Turner and *Cnephasia jactatana* Walker (Wearing 1994).

Charles *et al.* (1987) suggested that an Australian natural enemy could be introduced to New Zealand to control *E. phaulocosma* larvae in boysenberry crops where insecticide use is limited. *T. brevifacies* is an Australian species now known to attack *E. phaulocosma* on wild *Rubus* species. Therefore, further research into the effectiveness of *T. brevifacies* as a parasitoid of *E. phaulocosma* in commercial cane fruit crops might provide valuable results which may be important. *T. brevifacies* is already known to attack *E. postvittana* and *C. obliquana* (Green 1984), which are pests of cane fruits, and this parasitoid could be a useful component of integrated pest management programmes for these crops.

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REFERENCES

Cantrell, B. K., 1986: An updated catalogue for the Australian Tachinidae (Diptera). *Journal of Australian Entomology 25*: 255-265.

Charles, J. G; Dugdale, J. S & White, V., 1987: Preliminary studies of *Eutorna phaulocosma* (Lepidoptera: Oecophoridae) in New Zealand. *New Zealand Journal of Zoology 14*: 519-526.

Green, O. R., 1984: New Zealand host and locality records for an introduced tortricid parasite, *Trigonospila brevifacies* (Diptera: Tachinidae). *New Zealand Entomologist 8*: 69-71.

Penman, D. R., 1984: Deciduous tree fruit pests. Pp 271-308 *In* Scott, R.R. (Ed): *New Zealand Pest and Beneficial Insects*. Lincoln University College of Agriculture, Canterbury, New Zealand.

New Zealand Entomologist, 1997, Vol. 20, 71-72.

Singh, P., 1983: A general purpose laboratory diet mixture for rearing insects. *Insect Science and its Application 4*: 357-362.

Thomas, W. P., 1989: *Epiphyas postvittana*, the lightbrown apple moth. Pp. 187-195 *In* Cameron, P.J.; Hill, R.L.; Bain, J.; Thomas, W.P. (Eds): *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987*. CAB International, Wallingford, U.K.

Wearing, C.H., 1994: National Leafroller Survey: Species Distribution Charts for Crops and Regions. *HortResearch Internal Report No. IR 94-64*: 51.