

Non-target species selection for host-range testing of *Mastrus ridens*

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ABSTRACT

The approach taken to selecting non-target species for host-range testing of *Mastrus ridens* (= *M. ridibundus auct.*) (Hymenoptera: Ichneumonidae), a proposed biocontrol agent for codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae) in New Zealand, is described. An initial list of potential hosts was developed, derived from a combination of phylogenetic/taxonomic affinity to codling moth, ecological similarity to codling moth, and 'safeguard' or environmental considerations. The species selected, all in the family Tortricidae, were: *Cydia succedana* and *Grapholita molesta* (both exotic species in the sub-family Olethreutinae, tribe Grapholitini), the endemic "*Argyroplote*" *chlorosaris* (unassigned in the Olethreutinae), and the endemic *Ctenopseustis obliquana* and *Planotortrix octo* (both of which are common pest species in the sub-family Tortricinae, tribe Archipini).

Keywords. *Cydia pomonella*, codling moth, classical biological control, *Mastrus ridibundus*, Kazakhstan.

INTRODUCTION

Classical biological control of an exotic insect pest results from the successful, deliberate introduction of an exotic natural enemy (usually a parasitoid or predator) from the pest's country of origin. The risk that the new natural enemy will attack native insect fauna, and hence pose an unwanted environmental threat, is assessed by host-range testing in a quarantine laboratory before it is considered for release into its new environment. Such testing consists essentially of two parts:-(a) selecting a candidate list of non-target species and (b) exposing each candidate on the list to the natural enemy to determine experimentally if it is likely to be at risk if exposed to the new natural enemy in the wild. It is clearly impossible to test every insect that the natural enemy may encounter in its new environment, and the selection of species to expose to the new biocontrol agent is an important component of modern classical biocontrol programmes. In New Zealand, the release of new biocontrol agents is subject to regulatory approval, and so it is important that decisions of what species to include or omit from the list are rationally and transparently made.

The procedures for selecting appropriate non-target species are better established for weed biological control agents than for arthropod biological control agents (Messing 2001; Hoddle 2004), but progress has been made in recent years to improve them for the latter. No parasitoid successfully parasitises all hosts in the habitats it encounters. Those that it does attack share certain characteristics (most commonly taxonomic relatedness and similar ecology) which allow predictions of a biocontrol agent's

unknown host range to be made. A methodology for selecting non-target host species for exposure to proposed biocontrol agents based on known characteristics was placed on a scientific footing by Kuhlmann *et al.* (2006). In summary, an initial list of species is derived from criteria selected from the three categories of phylogenetic or taxonomic affinities with the target host, ecological similarities to the target host, and socioeconomic (or 'safeguard') considerations (which include possible threats posed by the natural enemy to native species). The weightings given to the different criteria will vary between programmes because it is generally accepted that selection of non-target test species has to be carried out on a case-by-case basis. The initial list can then be filtered (i.e., reduced) if appropriate by taking into account spatial, temporal and morphological attributes that might make a non-target inaccessible to the biocontrol agent. An additional filter can take into account the practicality of obtaining a non-target for testing. The non-target species in the list are then exposed to the proposed biocontrol agent, and any new information gathered is used to revise the list, so that additional species are tested if appropriate. This approach was used by Berndt *et al.* (2009) to select species for testing against *Cotesia urabae* (Austin & Allen) (Hymenoptera: Braconidae), a proposed biocontrol agent from Australia against *Uraba lugens* (Walker) (Lepidoptera: Noctuidae) in New Zealand.

Codling moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae: Olethreutinae: Grapholitini) (*Laspeyresia pomonella* in the older literature) is an old-world insect. Recent examination of global germplasm stocks and use of molecular marker techniques have confirmed that the domestic apple originated in Central Asia (Geibel *et al.* 2000; Harris *et al.* 2002), and so the very close association of codling moth with apple points to Central Asia as the origin of the pest as well (Mills 2005). Codling moth then spread almost globally with the development of apples and pears as a food source for early human populations and subsequently as internationally traded crops. It is currently present everywhere that apples are grown, with the notable exceptions of eastern China (including Taiwan), Japan and Western Australia (Mills 2005; Woods *et al.* 2001). Codling moth was accidentally introduced into New Zealand in the 1860s in apples imported from Tasmania and the USA (Miller 1953) and is now found throughout the country wherever apples are grown. It became a serious pest in orchards and domestic gardens soon after its arrival in New Zealand, and was one of the first targets for classical biological control in the late 18th and early 19th centuries. These initiatives were largely ineffective despite the establishment of two species of parasitoid (*Liotryphon caudatus*

(Ratzeburg) (Hymenoptera: Ichneumonidae) and *Ascogaster quadridentata* (Hymenoptera: Braconidae) (Wearing & Charles 1989)).

Recent foreign exploration (in the 1990s) together with the development of stage-structure modelling of codling moth population growth showed that more effective biocontrol of the pest could be achieved (Kuhlmann & Mills 1999; Mills 2005). As a result, *Mastrus ridibundus* Gravenhorst (Hymenoptera: Ichneumonidae: Cryptinae: Phygadeuontini) was released into California (Mills 2005). The parasitoid is found naturally in Central Asia (in southern Kazakhstan and north-western China in the foothills of the Tien Shan mountains) (Horstmann 2009, Mills 2005). Those released into California were collected from parasitised codling moths in apple orchards in Kazakhstan situated at elevations of 500-1000m a.s.l. at the base of the Tien Shan mountains (Mills NJ *pers. comm.*). *M. ridibundus* established in California and the Pacific North West from 1996, and was introduced from California to Argentina in 2003 and Chile in 2006 (Devotto *et al.* 2010). Descendants of the Kazakhstan colony were imported into New Zealand in January 2009 from a laboratory colony in Argentina, and a New Zealand colony established in quarantine at Plant & Food Research, Auckland, under ERMA New Zealand Approval Code NOC002518.

Subsequently, the specimens collected in Kazakhstan, together with laboratory reared specimens from the Argentinian colony, were re-examined and re-described as a new species, *M. ridens* (Horstmann 2009). Hence this is the species brought into quarantine in New Zealand. *M. ridibundus* remains a valid species in the western Palaearctic region, but it does not occur in Kazakhstan and does not attack codling moth (Horstmann 2009).

This paper describes how a list of non-target species was derived for exposure to *Mastrus ridens* Horstmann, a potential biocontrol agent for codling moth in New Zealand.

MATERIALS AND METHODS

Systematic studies of the New Zealand species of Lepidoptera were used to identify those species that are most closely related to codling moth. The biology of *Mastrus ridens* was examined in order to seek ecological features that might attract female parasitoids to non-target species. Then information on the biology of the moths most closely related to codling moth was gathered to identify the ecological traits in common with codling moth that might be recognised by *Mastrus ridens*. Shared traits of feeding and pupal biology were particularly sought. The moths that were closely related to codling moth were also assessed for their socioeconomic values, especially those relating to conservation. A combination of taxonomic relatedness and ecological similarity to codling moth, and 'safeguard' or socioeconomic criteria was then used to develop an initial list of non-target hosts that should be exposed to *M. ridens* in quarantine experiments in New Zealand.

RESULTS

Phylogenetic and taxonomic affinities to codling moth of non-target hosts

Codling moth is the only known host of *M. ridens* in Kazakhstan

and in California and Washington State (Kuhlmann & Mills 1999, Horstmann 2009, Nick Mills *pers. comm.*). These field records are supplemented by several quarantine laboratory experiments on non-target hosts, the results of which were summarised in an 'Environmental Assessment' report prepared to gain approval to release *M. ridens* into the USA (Hennessey *et al.* 1995). The experiments showed that *M. ridens* successfully parasitised the lesser appleworm *Cydia prunivora* (Walsh), but developed abnormally. *M. ridens* did not parasitise any of the following species of Tortricinae (all in the tribe Archipini): the rose tortrix, *Archips rosana* (L.); the orange tortrix, *Argyrotaenia citrana* (Fernald); the forest tortricid, *Pandemis chondrillana* (H.-S.); the oblique-banded leafroller, *Choristoneura rosaceana* (Harris). Hence "evidence from several sources indicates that *M. ridens* is specific to codling moth and perhaps other members of the tortricid tribe Grapholitini" (Hennessey *et al.* 1995).

Tortricidae (leafrollers) consists of three subfamilies, Tortricinae, Olethreutinae, and Chlidanotinae (as in Dugdale 1988) with each further divided into several tribes. In New Zealand, the Chlidanotinae is represented by a single species, *Lopharcha insolita* Dugdale. This species is endophytic in the fruit of the endemic forest tree *Litsea calicularis* (Lauraceae), but has a caterpillar less than half the size of codling moth. In view of the apparent host specificity exhibited by *M. ridens* both in the field and in laboratory experiments it was considered appropriate to limit potential non-target hosts in this assessment to species in the Olethreutinae. Horak (2006) used a morphology-based phylogenetic analysis of the Australian Olethreutinae to clarify details of tribal relationships within the subfamily and discussed tribal assignment of the New Zealand genera (as listed in Dugdale 1988). This analysis has allowed assignment of the New Zealand Olethreutine species to tribes (Table 1).

Codling moth is in the tribe Grapholitini, and so its closest relatives in New Zealand are the two other species in the tribe, both of which are adventive (i.e., exotic) to New Zealand. *Grapholita molesta* (oriental fruit moth) is an important pest of fruit crops, and *Cydia succedana* (gorse pod moth) is a biocontrol agent introduced in 1992 to control gorse (Hill & Gourlay 2002).

The two tribes most closely related to the Grapholitini are Enarmoniini and Eucosmini, but there are no species of Enarmoniini in New Zealand. Hence, from a phylogenetic perspective, species from the Eucosmini are the most closely related to codling moth and others in the Grapholitini. There are 16 species of Eucosmini in New Zealand, of which nine are endemic, four are adventive and three are indigenous. The *Crociosema* species are more closely related to the Grapholitini than to all other Eucosmini (Horak 2006), but they are not endemic.

The remaining two olethreutine tribes, Olethreutini and Microcorsini, are phylogenetically basal to Enarmoniini, and so are most distantly related to codling moth. Two endemic New Zealand species ("*Argyroploce*" *chlorosaris* and "*Strepsicrates*" *sideritis*) are currently not assigned to tribes.

The New Zealand tortricid fauna is represented by more species in the Tortricinae than in the Olethreutinae. Two of the tortricines, the endemic *Ctenopseustis obliquana* Walker and *Planotortrix octo* Dugdale, are also pests of pipfruit crops, and one or other (or both) are often found on the same trees as codling moth. They pupate in cocoons within the foliage. Both species are in the Archipini – from which tribe most other non-target species for testing against *M. ridens* in other countries have been selected.

The biology of *Mastrus ridens*

M. ridens is a gregarious, idiobiont, larval ectoparasitoid, and females attack mature codling moth larvae or pre-pupae in their cocoons, laying several eggs anywhere on the cuticle. Such exploitation of a cocooned host is a well recognised evolutionary development within many (or most) species of the Cryptinae (Gauld 1988). Idiobiont larval ectoparasitoids typically attack hosts in concealed feeding or cocooning niches where the death or permanent paralysis of the host is less likely to increase the risk of predation (of both host and immature parasitoid) (Hawkins 1990). Hence the evolutionary biology of *M. ridens* indicates that females are likely to first search for suitable host habitat and then search for cryptic hosts within it (Gauld 1988), and they are unlikely to attack hosts that do not spin cocoons in which to pupate, or that cocoon in open or relatively unprotected habitats such as on foliage.

Species of *Mastrus* apparently may be facultative hyperparasitoids, but this trait has never been recorded by *M. ridens* (Kuhlmann & Mills 1999). In laboratory tests in the USA, conducted as

part of an environmental assessment of the parasitoid, it did not attack the following hymenopteran parasitoids: Bethyloidea: *Goniozus legneri* Gordh (on navel orangeworm, *Amyelois transitella*); Braconidae: *Ascogaster quadridentatus* Wesm. (on codling moth), *Microdus refipes* (Nees) (on codling moth); Ichneumonidae: *Liotryphon caudatus* (Ratz.) (on codling moth), *L. extensor* (Tasch.) (on codling moth), *Venturia canescens* (Grav.) (on Mediterranean flour moth, *Ephestia kuehniella*) (Hennessey *et al.* 1995). Hence it was not considered necessary here to carry out further tests to assess whether *M. ridens* would be a facultative hyperparasitoid.

Ecological similarity of non-target hosts to codling moth, and ecological availability for parasitism

Geographical distribution. *M. ridens* has established in numerous release locations in California and Washington State, USA (Mills 2005). In New Zealand, it can be expected to search for codling moth over wide areas and so be found in a variety of environments.

Codling moth occurs throughout the country, so it is considered unlikely that there will be any geographical restrictions on the presence of the parasitoid, except at altitudes high enough to limit the growth of apple trees. Hence it is unlikely that any non-target host within the Olethreutinae, except possibly *Acroclita discariana*, will be geographically isolated from attack by *M. ridens*.

Seasonal distribution. Codling moth is predominantly univoltine in the main apple growing regions of New Zealand (Hawke's Bay and Nelson), with an occasional partial second

Table 1. The New Zealand tribes and 25 species of Olethreutinae. Fourteen species are endemic (E), eight are adventive (A) and three indigenous species (I) are naturally shared with Australia.

	Origin	Host; Comments
Tribe: Grapholitini		
<i>Cydia pomonella</i> (Linnaeus)	A	Rosaceae fruit, flesh, seeds. Walnuts. Pupates on trunk or at base of host.
<i>Cydia succedana</i> (Denis & Schiffermüller)	A	<i>Ulex europaeus</i> (gorse), exotic Fabaceae (Genisteeae and Loteae). Larvae endophytic on seed pods. Pupates on gorse stems or in ground.
<i>Grapholita molesta</i> (Busck, in Quaintance & Wood)	A	Rosaceae shoots and fruit (usually stonefruit). Pupates in tree or at base of trunk.
Tribe: Enarmoniini	-	Not present in New Zealand
Tribe: Eucosmini		
<i>Acroclita discariana</i> Philpott	E	<i>Discaria toumatou</i> (matagouri). Largely confined to intermontane Canterbury-inland Marlborough. Overwinters and pupates on host
<i>Crociosema plebejana</i> Zeller	A	Adventive Malvaceae. PIWOH
<i>Crociosema</i> sp. indet.	I	<i>Chenopodium</i> sp.. Coastal. PIWOH
<i>Hendecasticha aethaliana</i> Meyrick	E	Moist swards. Biology unknown
<i>Holocola</i> sp. indet., <i>triangulana</i> group	A	<i>Acacia longifolia</i> (Sydney golden wattle). Coastal plantings. PIWOH

Table 1. Continued

<i>Holocola zopherana</i> (Meyrick)	I	<i>Kunzea ericoides</i> (kanuka), <i>Leptospermum</i> sp. (manuka). PIWOH
<i>Parienia mochlophorana</i> (Meyrick)	E	Semi-aquatic. On surface debris and seepages. Pupates in turf
<i>Protithona fugitivana</i> Meyrick	E	Semi-aquatic. On surface debris and seepages. Pupates in turf
<i>Protithona potamias</i> (Meyrick)	E	Riparian seepage turf. Pupates in turf
<i>Strepsicrates charopa</i> Meyrick	E	<i>Leptospermum</i> . Localised. PIWOH
<i>Strepsicrates doloepa</i> Meyrick	E	Host unknown. Localised
<i>Strepsicrates ejectana</i> (Walker)	I	<i>Calluna vulgaris</i> (heather), <i>Kunzea</i> , <i>Leptospermum</i> . Widespread. PIWOH
<i>Strepsicrates emplasta</i> Meyrick	E	<i>Coprosma</i> spp.. Widespread. PIWOH
<i>Strepsicrates infensa</i> (Meyrick)	A	<i>Eucalyptus</i> spp.. PIWOH
<i>Strepsicrates macropetana</i> (Meyrick)	A	<i>Eucalyptus</i> spp.. PIWOH
<i>Strepsicrates parthenia</i> Meyrick	E	<i>Leucopogon fasciculatus</i> (tall mingimingi). Mainly in scrub/bush areas. PIWOH
Tribe: Olethreutini: Zomaria group		
<i>Zomaria doxasticana</i> (Meyrick)	A	<i>Acacia</i> spp.. PIWOH
Tribe: Olethreutini; (includes Bactrini)		
<i>Bactra noteraula</i> Walsingham	E	Cyperaceae (sedges). Largely coastal. Larvae endophytic. Pupates at base of host.
<i>Bactra optanius</i> Meyrick	E	Cyperaceae and other sedge allies. Widely distributed in swampy/mire areas. Pupates in host turf.
Tribe: Microcorsini		
<i>Cryptasasma querula</i> Meyrick	E	Larvae feed on endosperm of large-seeded angiosperm trees (e.g. <i>Beilschmiedia</i> , <i>Quercus</i>). Pupates in litter.
Unassigned tribe		
“ <i>Argyroplce</i> ” <i>chlorosaris</i> Meyrick	E	<i>Metrosideros excelsa</i> (pohutukawa, a dry-fruited Myrtaceae). Endophytic in seed capsules.
“ <i>Strepsicrates</i> ” <i>sideritis</i> (Meyrick)	E	Not unlike Olethreutini. Found in dry forest litter. Larval biology unknown.

PIWOH = pupates in workings on host.

generation in warm years (Wearing 1979), but is bi-voltine (with occasionally a partial third generation) in the north of North Island (Wearing & Charles 1978). Neonate larvae bore into fruit of any age, feeding on seeds as well as the flesh, and emerge only when fully mature. The mature fifth instar larva spins a cocoon in which it pupates either within a few days during the summer or in spring after winter diapause. Where codling moth is univoltine, the species spends autumn, winter and early spring in diapause as a cocooned pre-pupal stage. In the summer generations of bi-

voltine populations the pre-pupal stage is short, with the second generation adults emerging usually after 2-3 weeks. Although all generations in New Zealand are synchronised to a significant extent by diapause and tree dormancy, some cocooned fifth instars can be found throughout the year (Wearing 1979; Wearing & Charles 1978). This is the stage that is attacked by female *M. ridens*, and their omnipresence should also allow *M. ridens* to be present throughout the year, which means that there is unlikely to be any seasonal ‘refuge’ for potential non-target hosts.

Life-history attributes

Most of New Zealand's native olethreutines are not found in apple orchards or modified habitats where codling moth are found (Table 1). So potential non-target, native hosts are only likely to be encountered by *M. ridens* when female parasitoids disperse in search of new hosts. It is reasonable to assume that these parasitoids are most likely to begin searching for hosts on trees that have apparent similarities to apples and will then respond to potential non-target species that have pupation behaviour and cocooning sites similar to codling moth (e.g., Shaw 1994). The biology and ecology of most of New Zealand's olethreutine fauna are rather poorly known, but knowledge of their host plants and feeding or pupating behaviour (often gleaned from collection records) were compared with codling moth:

Host plants. The host plants in New Zealand of the three species of Grapholitini are well known (Table 1), and are largely restricted to the Rosaceae and gorse, although *Cydia succedana* has been found also on several species of exotic Fabaceae (Withers *et al.* 2008). None of the Grapholitini species is known from any native plants, but codling moth is known as a pest of walnut (*Juglans regia* L. (Juglandaceae)) (Wearing *et al.* 2001). Within the Eucosmini, the adventive species are restricted to Australian gums and wattles, and exotic Malvaceae, while the indigenous species are restricted to kanuka, manuka and exotic weeds (Table 1). Of the nine endemic species, four are from low lying plants associated with very wet conditions. One is widespread from *Coprosma* spp, one is from kanuka and manuka, one is from matagouri (a native buckthorn), one on tall mingimingi and there is no known host plant for one species (Table 1). Within the Olethreutini, the adventive *Zomaria doxasticana* has been recorded from wattles. The two endemic *Bactra* species are restricted to native sedges and relatives in open or swampy areas, while *Cryptaspasma querula* larvae feed on the large seeds in the drupes of tawa and taraire, and on oak acorns, and pupate in the

litter. "*Argyroploce*" *chlorosaris* has recently been reared from *Metrosideros excelsa* (pohutukawa, Myrtaceae) seed capsules (Martin NA, pers. comm.). The host niche of "*Strepsicrates*" *sideritis* in dry forest litter that apparently lacks hepatics and mosses is unknown (Table 1).

Feeding and pupation sites. Codling moth larvae are endophytic in the fruit but larvae usually crawl away from their feeding sites and spin their cocoons in cracks and crevices among branches or under the bark of the tree, or in the soil close to the tree trunk. There is evidence that *M. ridens* females improve their search efficiency by responding to a kairomone produced by the silken thread of newly spun codling moth cocoons (Jumean *et al.* 2005), and it seems probable that *M. ridens* females have evolved to search for their hosts in sites among bark or dried fruit remains, rather than among living leaves or fruits. Both *Cydia succedana* and *Grapholita molesta* larvae pupate in similar locations to codling moth – e.g., either on the bark or in mummified/dead fruit, or on the ground. By contrast to the Grapholitini, larvae of the Eucosmini and Olethreutini feed on host-plant foliage and pupate among the larval debris on their host (PIWOH in Table 1) or within the plant turf. In the Microcorsini, *Cryptaspasma querula* are considered to live (and pupate) among leaf litter on the ground. It is unknown where "*Argyroploce*" *chlorosaris* larvae pupate.

Socioeconomic ('safeguard') considerations

As discussed above, *Cydia succedana* is a valued exotic species because of its status as an introduced biocontrol agent for gorse. "*Argyroploce*" *chlorosaris* is an endemic insect with a unique association with the native tree *Metrosideros excelsa* (pohutukawa). It is a common insect in Auckland and could even be considered a 'pest' of its host because it destroys many seed capsules. However, its national distribution and population ecology is unknown, and significant ecological disturbance by an exotic parasitoid could have unknown consequences.

Table 2: Non-target species of Tortricidae selected for host-range testing of *Mastrus ridens*, a potential biological control agent for codling moth, *Cydia pomonella*.

Species	Subfamily: Tribe	Status	Host plant	Category that triggered inclusion
<i>Cydia succedana</i>	Olethreutinae: Grapholitini	Introduced biocontrol agent	Gorse, <i>Ulex europaeus</i> . Exotic Fabaceae	same tribe, shared host plant, socioeconomic
<i>Grapholita molesta</i>	Olethreutinae: Grapholitini	Introduced pest	polyphagous (Rosaceae)	same tribe, shared host plant
" <i>Argyroploce chlorosaris</i> "	Olethreutinae: Eucosmini (?)	Endemic	Pohutukawa, <i>Metrosideros excelsa</i>	shared host plant, socioeconomic
<i>Planotortrix octo</i>	Tortricinae: Arcipini	Endemic pest of fruit crops	polyphagous	related subfamily, shared host plant
<i>Ctenopseustis obliquana</i>	Tortricinae: Arcipini	Endemic pest of fruit crops	polyphagous	related subfamily, shared host plant

Development of an initial list for host-testing

As a result of the considerations above, an initial list of five non-target species for host-range testing of *M. ridens* was selected (Table 2). The apparent host specificity of *M. ridens* to codling moth from known worldwide data allowed the potential host range to be limited to the Olethreutinae. Within that sub-family, species were selected primarily on ecological characteristics and then on conservation value. The exotic *Cydia succedana* and *Grapholita molesta* were selected because they are the most closely related species to codling moth in New Zealand, and their cocoons are either present on apple trees (*G. molesta*) or close to orchards (in gorse patches which are a common rural occurrence) and so also likely to be encountered by *M. ridens* females searching for codling moths. Although *G. molesta* is regarded as a pest, *C. succedana* is a valued, introduced biocontrol agent for gorse. The endemic “*Argyroploce*” *chlorosaris* and *Cryptaspasma querula* were also considered possible candidates for testing. Although their relatedness to codling moth is less certain or more distant than most other native New Zealand olethreutines (the former is unassigned to a tribe, and the latter is in the most distantly related Microcorsini), they both have some ecological similarity to codling moth. The larvae of both species are associated with large trees (as opposed to low shrubs or weeds) and are endophytic within either seed capsules or fruits. In addition, the native host plants of both species (pohutukawa and tawa respectively) are highly valued by New Zealand society. Despite their similar ecology, only “*Argyroploce*” *chlorosaris* was selected for testing. This species is known only from pohutukawa, which is a highly valued tree both in the wild and as an ornamental. It is widespread in New Zealand so is likely to be encountered by *M. ridens*, especially in urban areas in northern New Zealand where there are many ‘backyard’ apple trees. *C. querula* has also become widespread on introduced oak trees, and so is perhaps less likely to be threatened if it were attacked.

Ctenopseustis obliquana and *Planotortrix octo* were also selected. These are of similar (distant) phylogenetic relatedness as other tortricid species found not to be hosts of *M. ridens* in other host-testing experiments, but are both common pests in New Zealand apple orchards and so have some ecological similarity to codling moth. However, their larvae are only rarely endophytic on fruits, and their larvae usually pupate among leaf debris so are unlikely to be sought by female *M. ridens*. Nevertheless, they were readily available throughout the year from laboratory colonies at Mt Albert Research Centre and so were considered to be useful to help with the design of experimental protocols. They should also provide results comparable with those of North American Archipini vis-s-vis parasitism (or lack of it) by *M. ridens*.

The remaining Olethreutini were not considered to be at risk from *M. ridens* on ecological grounds either because their host plants were too dissimilar to apple trees (e.g., grasses, annual weeds, sedges, Myrtaceae), or because they did not pupate in areas that *M. ridens* would be searching (PIWOH in table 1). The adventive species were also considered to be of little conservation value. Two species (*Hendecasticha aethaliana* and “*Strepsicrates*” *sideritis*) were rejected because so little was known about their biology that it was not considered feasible to

find or rear them within the logistical limits of the biocontrol programme. Nevertheless, nothing about their known biology indicated that they would be particularly attractive to *M. ridens*.

DISCUSSION AND CONCLUSIONS

If released into New Zealand, *M. ridens* is expected to establish throughout the country, wherever codling moth is present, and to overlap the distribution of most of New Zealand’s tortricids. As codling moth is the only known host of *M. ridens* in the wild, the list of potential non-target species for testing against *M. ridens* was limited to three species of Olethreutinae selected on the basis of close phylogenetic relatedness to codling moth, ecological similarity to codling moth or socioeconomic considerations. Two species of Tortricinae were also selected primarily because of practical considerations – especially their ready availability.

Proposed larval ectoparasitoid biocontrol agents such as *M. ridens* do not have to overcome active biochemical or physiological host defences (as do koinobiont larval endoparasitoids), and so their host range is likely to be more influenced by host ecology than by host taxonomy (Kuhlmann *et al.* 2006; Shaw 1994). This poses a real challenge for non-target host-testing trials, because it is likely that many of the natural cues that affect host-selection and oviposition behaviour of these parasitoids will be absent from the enclosed and artificial environments of quarantine laboratories. As a result, we hypothesise that non-target host-testing trials with *M. ridens* in quarantine will overestimate its ecological host range (i.e., the species it will attack if released into New Zealand). If the results of those host-testing experiments point to specific ecological traits used by *M. ridens*, then the list presented here may be supplemented to reflect that additional information. However, empirical evidence suggests that idiobiont larval ectoparasitoids of ecologically isolated hosts attack few other species, and, in at least some cases, it appears that ecological restrictions can very effectively limit their host range (Kuhlmann *et al.* 2006).

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