Manaaki Whenua
Landcare Research

Feasibility of successful biological control of paper wasps, *Polistes spp*.

Envirolink Grant: C09X2006 2133-NLCC116

Prepared for: Nelson City Council

May 2021

Feasibility of successful biological control of paper wasps, *Polistes spp*.

Contract Report: LC3971

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Contents

Summary

Project and client

- This Envirolink project (2133-NLCC116) was initiated by Nelson City Council.

Objectives

- The objective of this report was to summarise information from the literature on the potential options for biological control of the three species of invasive paper wasps (*Polistes* spp.) in New Zealand.

Methods

- We used Web of Science, Google Scholar, CAB Direct as well as literature already in our possession to obtain information on parasitoids and predators of *Polistes.*

Results

- The evidence from the literature indicates that there are many promising biological control options for *Polistes*.
- Since *Polistes* nest in the open, they are much more susceptible to parasitoids and nest scavengers than other social wasps that have enclosed nests, such as *Vespula.*

Conclusions

- Biological control has strong potential to control *Polistes* wasp populations over landscape scale in New Zealand.

Recommendations

Research needs

- Surveys of colonies of the three species of *Polistes* should be carried out to determine if there are natural enemies already present in New Zealand that could be augmented.
- If there are no natural enemies present in New Zealand, there are two options available:
    - classical biological control using natural enemies from the home range of each of the targeted *Polistes* species
    - new association classical biological control using natural enemies that are more plastic in their host range but still specific to the *Polistes* genus.

Priority biocontrol agents

- *Chalcoela* moths (Lepidoptera: Crambidae): investigate the attack efficacy of the two moth species (*Chalcoela iphitalis* and *C. pegasalis*) known to severely damage colonies of many species of *Polistes,* including *P. dominula* in North America.
    - Estimated costs: $500,000–$750,000
- Ichneumon wasp: *Latibulus argiolus* is a parasitoid wasp known to damage colonies of *Polistes dominula* in its home range, but research is needed to confirm attack on *P. chinensis antennalis* and *P. humilis.*
    - Estimated costs: $500,000–$750,000
- Eulophid wasp: *Elasmus schmitti* is a small parasitoid wasp known to attack *P. dominula* in Europe, but research is needed to confirm attack on *P. chinensis antennalis* and *P. humilis.*
    - Estimated costs: $500,000–$750,000

1 Introduction

1.1 Paper wasps in New Zealand

Paper wasps are a group of social wasps from the Polistinae subfamily of Vespidae (Hymenoptera: Vespidae: Polistinae). New Zealand has no native Vespids, but three exotic species of paper wasp have now established: *Polistes chinensis antennalis*, *P. dominula*, and *P. humilis.* Other Vespidae wasps established in New Zealand are the social German wasp (*Vespula germanica*) and common wasp (*V. vulgaris*), as well as the solitary European tube wasp (*Ancistrocerus gazella*).

The Australian paper wasp, *Polistes humilis*, was the first species of paper wasp to establish in New Zealand. It is now found in the northern two-thirds of the North Island and is thought to have reached its maximum suitable habitat range. The second paper wasp to invade New Zealand was the Asian paper wasp, *Polistes chinensis antennalis,* which is also the most widespread. The current range of *P. chinensis antennalis* is virtually the whole North Island as well as the top of the South Island. There have also been some found as far south as Dunedin. This species may still be expanding its range.

The most recent arrival is the European paper wasp, *P. dominula*. This species was first observed in 2013 in Blenheim (Haw 2016) and has since been found in the Auckland area, Tasman region, Hanmer Springs, Christchurch, Temuka and Alexandra (Global Biodiversity Information Facility database [GBIF.org]). *P. dominula* is still in the very early stages of its range expansion in New Zealand. A recent study has predicted the suitable habitat to include nearly all of the North Island and the eastern side of the Southern Alps in the South Island (Howse et al. 2020).

1.2 Impacts

Paper wasps are generalist predators of a wide range of invertebrates, but mostly prefer lepidopteran caterpillars (Clapperton 1999). Unlike the other invasive wasps (*Vespula* spp.), they do not normally scavenge for dead types of protein, such as lunch meat at a picnic or road kill. However, like other wasps they do require carbohydrates and will forage for sugar from flower nectar, fruits, and insect-produced honeydew (Clapperton 1999).

At Lake Ohia, in the far north of the North Island, wasp nest densities can vary between 20 and 210 nests per hectare (Clapperton 1999). In areas of the highest nest densities it was estimated that paper wasps consumed 957 g/ha of invertebrate biomass each year (Clapperton 1999). Clapperton estimated that the paper wasp's impacts in the far north are similar to those of *Vespula* spp. in scrubland and pasture.

Paper wasps may provide limited beneficial effects in some sectors, acting as biological control agents of lepidopterous pests (Todd et al 2015), but they also have adverse effects by preying on dozens of native species (Ward & Ramon-Luca 2013). Their preference for lepidopteran larvae means paper wasps are often disliked because they readily prey upon monarch butterfly (*Danaus plexipus*) caterpillars (Clapperton 1999). In addition, general predation by *Polistes* and *Vespula* has been listed as a potential factor contributing to the

poor or slow establishment of some weed biocontrol agents, such as the Honshu white admiral butterfly (*Limenitis glorifica*) and the broom leaf beetle (*Gonioctena olivacea*) (Paynter et al. 2019).

Where they are prevalent, paper wasps can also directly affect people. This is usually due to the wasps' preference for building nests under the eaves of houses, in sheds, or in garden shrubs, where they can easily be accidently disturbed. All three species of paper wasps will defend their colony if it is disturbed, which is the most common cause of stings. Although paper wasp nests are much smaller than *Vespula* nests, paper wasp nests are often more numerous in a given area (Clapperton 1999), which may increase the chances of people inadvertently coming into contact with a nest. Even before the addition of the European paper wasp to New Zealand, paper wasps accounted for most of the insect stings received by Aucklanders in a 1992/93 survey (Dymock et al. 1994).

1.3 Current control

The only effective treatment is direct application of insecticide to the nests. Unlike *Vespula*, paper wasps are not attracted to protein baits like Vespex, since they do not scavenge for protein. Paper wasps are attracted to fermentation odours, but since many beneficial insects are too, trapping with synthetic sweet and fermented lures is not viable for large-scale use. While direct poisoning of nests is efficient at a small scale, it is not a viable control method at a landscape scale.

2 Objectives

The aim of this review project is to identify putative classical biological control agents to regulate the populations of the three invasive *Polistes* species currently found in New Zealand.

3 Methods

Literature was searched using Web of Science, Google Scholar, and CAB Direct, as well as literature already in our possession, to obtain information on parasitoids and predators of *Polistes.* The search terms used were: "*Polistes chinensis antennalis*" OR "*Polistes chinensis*" OR "*Polistes dominula*" OR "*Polistes dominulus*" OR "*Polistes humilis*" AND "parasitoid" OR "predator" OR "parasite" OR "inquiline" OR "natural enemy". Generalist predators such as birds and hornets were rejected from the review. Species that are likely to be hyperparasitoids of other nest visitors were also excluded. Only species with a host specificity of at least the Polistinae subfamily level, or more specific, were considered as potential agents.

4 Results

A review of the current literature provides a lot of information on the nest visitors, social parasites and parasitoids of many species of *Polistes* from around the Northern Hemisphere. Most of the published studies on natural enemies of *Polistes* are from North America (for example Rau 1941; Nelson 1968), but there have also been several from Japan (Makino 1983, 1985, 1989) as well as studies on the impacts of parasitoids on the populations of *Polistes* in Eastern Europe (Rusina 2008, 2013). Unfortunately, parasitoids associated with two of the species, *P. humilis* and *P. chinensis antennalis,* are poorly represented in the literature. However, for *P. dominula* there were many published studies, both from its native range and from its invaded range. A list of parasites associated with *Polistes* can be found in the Appendix.

4.1 Diptera

There are several species of fly known to attack *Polistes*. The most relevant are from two genera of Tachinids that are known to attack the three *Polistes* species currently present in New Zealand. *Anacamptomyia nigriventris* has been described as a parasitoid of *P. humilis* (Makino 1985) and *Anacamptomyia* sp. has been found to attack *P. dominula* in South Africa (Benadé et al. 2014). *Euvesporia decipiens* is known to parasitise *P. chinensis antennalis* as well as several other species of *Polistes*, along with *Vespa mandarina* and *Vespa simillima* (Takahashi et al. 2008). While these Tachinid species were recorded from *Polistes* nests, there is very little information on their biology or impacts on the colonies.

4.2 Hymenoptera

There are at least 27 species of Hymenoptera, from the Chalcididae, Eulophidae, Ichneumonidae, Mutillidae, Toyrmidae, and Trigonalidae families, from all over the world, found to be associated with *Polistes* nests (Yamane 1996). Many of these are likely to be parasitoids or hyperparasitoids of other nest visitors, such as the Lepidopteran scavengers and parasitoids. Of the families listed above, the Ichneumonidae and Eulophidae are the best-studied parasitoids of *Polistes*.

The Eulophid genus of *Elasmas* has four species that parasitise 10 species of *Polistes*. These are small, gregarious ectoparasitoid wasps that lay multiple eggs on the surface of their host larvae as they are beginning to spin their cap for pupation (Reed & Vinson 1979; Gumovsky et al. 2007). Overwintering takes place as pupae in the deserted nest (Strassmann 1981b). *Elasmus schmitti* is a well-known parasitoid of *P. dominula* (as well as *P. gallicus, P. omissus,* and *P. nimphus*) in its European home range (Gumovsky et al. 2007; Makino 1985). Rusina (2013) found *E. schmitti* parasitising between 7.9 and 42.9 % of *P. dominula* nests surveyed between 2006 and 2010 at sites in Ukraine and Russia.

In the Americas, *Elasmus polistis* attacks at least five species of *Polistes*: *P. annularis*, *P. exclamans*, *P. fuscatus*, *P. metricus* and *P. versicolor* (Strassmann 1981a; Makino 1985; Dorfey & Kohler 2011). While none of the three target species are among its known hosts, the broad range of hosts within the *Polistes* genus by *E. polistis* suggests that this ichneumon wasp may be able to attack them if it were to encounter them. In Europe,

E. schmitti is hyper-parasitised by another Eulophid, *Baryscapus elasmi* (Gumovsky et al. 2007). It is likely that without these hyperparasitoids, *E. schmitti* would demonstrate a higher incidence of parasitism of *Polistes* nests.

The ichneumonid genus *Latibulus* has at least five species that are parasitoids of various *Polistes* species. These parasitoids look very similar to their hosts, having a black (or dark brown) body with yellow markings. Similar to their close relatives, *Sphecophaga* spp. (a parasitoid of *Vespula* wasps), *Latibulus* have both overwintering and summer forms of adults, as well as two forms of cocoons (Oh et al. 2012). The summer form adults emerge from dark orange to light brown-coloured soft cocoons, while the winter form imagoes emerge from hard, thick-walled, brown cocoons (Oh et al. 2012). The best known of these is *L. argiolus*, which parasitises at least five species of *Polistes* in its Palearctic distribution (Rusina 2008, 2011; Makino 1985). Rusina (2013) found that the abundance of *Polistes dominula, P. gallicus* and *P. nimpha* was regulated by *L. argiolus,* the magnitude of which depended on how early the colonies were infested. In some study sites more than 80% of nests were parasitised by *L. argiolus,* with up to 34% strongly parasitised (greater than 10% of cells infested) (Rusina 2013). Although the species was not identifiable, several cocoons of *Latibulus* sp. have been found in the nests of *P. chinensis antennalis* in Mongolia (Oh et al. 2012).

Another ichneumonid, *Pachysomoides fulvus,* has a broad host range within *Polistes* and is known to attack at least 10 species (Makino 1985). Four other species of *Pachysomoides* have also been described from *Polistes* (Makino 1985). Unfortunately, no attack by *Pachysomoides* has yet been documented from any of the three species currently found in New Zealand. However, given the vast host range on *Polistes* in their native range in North and South America, they will probably also make new associations if they contact new *Polistes* species.

4.3 Lepidoptera

At least 11 species of moth are known to infest *Polistes* nests (Makino 1985). These species are from the Crambidae, Cosmopterygidae, Gelechiidae, Pyralidae, and Tineidae families, and most are scavengers within the nest. However, two species of *Chalcoela* (Crambidae) are brood parasites of at least 10 species of *Polistes.* These moths have been observed laying their eggs on substrate near wasp nests at night, often immediately after making antennal contact with the host wasp or nest (Nacko & Henderson 2017). Each *Chalcoela* larvae kills one pupal or pre-pupal wasp. However, holes between cells may indicate that some *Chalcoela iphitalis* larvae may feed on multiple pupae (Nacko & Henderson 2017).

The native range of *C. iphitalis* is North America, from southern Canada through Mexico (Nelson 1968). Infestations of *C. iphitalis* have proven capable of destroying a large percentage of wasp pupae in a short time, which is associated with nest decline (Strassmann 1981a; Nacko & Henderson 2017). In a 10-year study in North America there was no noticeable difference of infestation of the invasive *P. dominula* compared to the native *P. fuscatus* by *C. iphitalis*, both with infestation rates of up to 35% (Miller et al 2013). An earlier study found that *C. iphitalis* destroyed 40–73% of *P. exclamans* in the southern United States (Strassmann 1981a).

In eastern North America and the Caribbean, *Chalcoela pegasalis* (formerly *Dicymolomia pegasalis*) is also known to be an effective natural enemy of at least nine species of *Polistes*. Like *C. iphitalis*, *C. pegasalis* has never been recorded from any other host besides *Polistes* spp. (Nelson 1968). Its ability to attack multiple *Polistes* spp. could be particularly useful in New Zealand, where control of three *Polistes* spp. is currently needed.

Establishment of *Chalceola* spp. in New Zealand could also potentially provide protection against further incursions of additional *Polistes* spp. In the early 20th century *C. pegasalis* was described as a disease of *Polistes* in the West Indies (Ballou 1915, cited in Nelson 1968). Later reports claimed that *C. pegasalis* was responsible for eliminating *Polistes* from certain islands in the West Indies (Ballou 1919, 1934, cited in Nelson 1968). Rau (1941), from his observations of 200 *Polistes* colonies from various locations in Missouri, USA, found that *C. pegasalis* had parasitised 10% of nests, ranging from only one cell to as many as 50% of cells. Rau (1941) states that there are three generations per year: two in summer and one overwintering.

4.4 Strepsiptera

The endoparasitic insects in the genus *Xenos* (Strepsiptera: Xenidae) significantly alter the behaviour and physiology of their *Polistes* hosts (Beani et al 2018). The alterations to physiology include the castration of the parasitised future queens (Kathirithamby 2009) and off-season hibernation (Beani et al. 2018). Workers parasitised by *Xenos* do not perform their normal duties for the colony, such as rearing siblings or defending the nest, and instead act more like future queens by abandoning the nest to aggregate on nearby vegetation with other parasitised wasps (Beani et al 2018). Of the parasites so far mentioned, the life cycle of *Xenos* is the most complex. There are currently 24 *Xenos* species known to parasitise *Polistes* (Cook 2019; see Appendix).

Xenos vesparum is a well-studied species that parasitises *P. dominula.* The life cycle (as described in Beani et al. 2018) starts in spring, when the overwintered parasitised Polistes begin to forage. The triungulin larvae (phoretic first instar larvae) of *Xenos vesparum* are released from the abdomen of the *Polistes* while they wander over vegetation or nests. These triungulin larvae either directly infest the nest or are brought back to the nest by foraging workers. Once at the nest, the larvae infest the wasp larvae (at any stage). The parasitised wasps emerge as adults and soon abandon the nest, where the male *X. vesparum* emerge from pupae in the abdomens of the wasps and fly off to locate female *Xenos*, which are permanently endoparasitic on the wasps, and the first mating occurs. Male *Xenos* die shortly after mating. The second release of triungulins then occurs and results in further infestation of wasps. In late summer, the mating of the second generation occurs, and the parasitised wasps find a hibernaculum to overwinter in. While parasitism of the individual host wasps may not have a direct effect on host mortality (Hughes & Kathirithamby 2005), the castration of up to 25% of overwintering future queens means there will fewer queens able to found nests the following year (Hughes et al 2004). *Xenos* spp. are known to parasitise over 30 species of *Polistes* (Hughes et al. 2004).

5 Conclusions

Invasive *Polistes* are damaging to New Zealand's biodiversity and are a danger to human health due to their habit of nesting in man-made structures. However, since they are not perceived as pests to primary industries, there has historically been only a minor drive to control them. Without the financial backing of industry, the most cost-effective way to control paper wasps over a landscape scale is to use classical biological control.

The evidence from the literature indicates that there are many promising biological control options for the most recent arrival, *Polistes dominula.* Since many of the natural enemies mentioned above, which are specific to the subfamily level, do not exhibit a host specificity within the Polistinae, *P. humilis* and *P. chinensis antennalis* will probably be attacked. Because New Zealand does not have native Hymenoptera species within the Vespidae family, the host specificity at the subfamily level could be viewed as a positive attribute. Having classical biological control agents capable of attacking multiple species of *Polistes*, particularly as new associations, might be more cost-effective than using different species specific to each *Polistes* species, and could be instrumental in slowing establishment of any new *Polistes* arrivals in New Zealand.

6 Recommendations

6.1 Research needs

Surveys of colonies of the three species of *Polistes* should be carried out to determine if there are natural enemies already present in New Zealand that could be augmented. If there are no natural enemies already present in New Zealand, there are two options available:

- classical biological control using natural enemies from the home range of each of the targeted *Polistes* species
- new association classical biological control using natural enemies that are more plastic in their host range, but still specific to the *Polistes* genus (this is probably the most cost-effective option)

6.2 Priority biocontrol agents

- *Chalcoela* moths (Lepidoptera: Crambidae): investigate the attack efficacy of the two moth species (*Chalcoela iphitalis* and *C. pegasalis*) known to severely damage colonies of many species of *Polistes*, including *P. dominula* in North America.
    - Estimated costs: $500,000–$750,000
- Ichneumon wasp: *Latibulus argiolus* is a parasitoid wasp known to damage colonies of *Polistes dominula* in its home range, but research is needed to confirm attack on *P. chinensis antennalis* and *P. humilis.* Parasitism of *P. chinensis antennalis* by *Latibulus* sp. has been documented from Mongolia, but since the specimens were immature the authors were unable to determine the species (Oh et al. 2012).
    - Estimated costs: $500,000–$750,000

- Eulophid wasp: *Elasmus schmitti* is a small parasitoid wasp known to attack *P. dominula* in Europe, but research is needed to confirm attack on *P. chinensis antennalis* and *P. humilis.*
    - Estimated costs: $500,000–$750,000

7 Acknowledgements

Thanks to Quentin Paynter for peer review of this report. Thanks also to Nelson City Council for commissioning this report, and to MBIE for providing the Envirolink grant.

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Appendix – *Polistes* host–parasite associations

Natural enemy				Hosts		Life stage attacked	Notes	Refs
Order	**Family**	**Genus**	**Species**	**Genus**	**Species**			
Diptera								
1	Tachnidae	*Anacamptomyia*	*nigriventris*	***Polistes***	***humilis humilis***	brood/pupae		*Richards 1978 cited in* Makino 1985
				Polistes	*sp.*	brood/pupae		*Crosskey 1973 cited in* Makino 1985
2	Tachnidae	*Anacamptomyia*	*africana*	*Polistes*	*marginatus africanus*	brood/pupae		*Fitzgerald 1940 cited in* Makino 1985
		Anacamptomyia	*sp.*	***Polistes***	***dominula***	brood/pupae	syn *P. dominulus*	Benadé et al. 2014
		Anacamptomyia	*sp.*	*Polistes*	*marginalis*	brood/pupae		Benadé et al. 2014
3	Tachnidae	*Euvespivora*	*decipiens*	*Polistes*	*sp.*	brood/pupae		*Crosskey 1973 cited in* Makino 1985
				Polistes	***chinensis antennalis***	brood/pupae		Takahashi et al. 2008
				Polistes	*jokahamae*	brood/pupae		Takahashi et al. 2008
				Polistes	*snelleni*	brood/pupae		Takahashi et al. 2008
				Polistes	*rothneyi*	brood/pupae	also in *Vespa mandarina* & *V simillima*	Takahashi et al. 2008
				Polistes	*nipponensis*	brood/pupae		Takahashi et al. 2008
Hymenoptera								
1	Eulophidae	*Elasmus*	*polistis*	*Polistes*	*exclamans*	brood/pupae		Strassmann 1981a, 1981b
				Polistes	*annularis*	brood/pupae		*Burks 1971 cited in* Makino 1985
				Polistes	*fuscatus*	brood/pupae		*Burks 1971 cited in* Makino 1985
				Polistes	*metricus*	brood/pupae		*Reed & Vinson 1979 cited in* Makino 1985
				Polistes	*versicolor*	brood/pupae		Dorfey & Kohler 2011

Natural enemy				Hosts		Life stage attacked	Notes	Refs
Order	Family	Genus	Species	Genus	Species			
2	Eulophidae	*Elasmus*	*japonicus*	*Polistes*	*jadwigae*	brood/pupae		*Iwata & Tachikawa 1966 cited in* Makino 1985
				Polistes	*riparius*	brood/pupae	1983 mis-id as *P. biglumis*	Makino 1983
				Polistes	*snelleni*	brood/pupae		Makino 1983
3	Eulophidae	*Elasmus*	*schmitti*	*Polistes*	*gallicus*	brood/pupae	poss mis-id *P.* dominula	*Guiglia 1972 cited in* Makino 1985
				Polistes	*omissus*	brood/pupae	syn *E. invreae*	*Guiglia 1972 cited in* Makino 1985
				Polistes	***dominula***	brood/pupae	syn *P. dominulus*	Gumovsky et al. 2007; Rusina 2013
				Polistes	*nimphus*	brood/pupae	syn *P. nimpha*	Gumovsky et al. 2007
4	Eulophidae	*Elasmus*	*biroi*	*Polistes*	*opinabilis*	brood/pupae		*Burks 1971 cited in* Makino 1985
5	Ichneumonidae	*Latibulus*	*argiolus*	*Polistes*	*gallicus*	brood/pupae	poss mis-id ***P.* dominula**	*Guiglia 1972 cited in* Makino 1985
				Polistes	*riparius*	brood/pupae	1983 mis-id as *P. biglumis*	Makino 1983, 1989
				Polistes	*snelleni*	brood/pupae		Makino 1983
				Polistes	***dominula***	brood/pupae		Rusina 2008, 2013
				Polistes	*nimphus*	brood/pupae		Rusina 2011
6	Ichneumonidae	*Latibulus*	*hokkaidensis*	*Polistes*	*riparius*	brood/pupae		Lee & Oh 2006
7	Ichneumonidae	*Latibulus*	*flavopetiolus*	*Polistes*	*rothneyi koreanus*	brood/pupae		Oh et al. 2012
		Latibulus	*sp.*	***Polistes***	***chinensis antennalis***	brood/pupae	unable to id *L.* to spc (Mongolia)	Oh et al. 2012
8	Ichneumonidae	*Latibulus*	*siculus*	*Polistes*	*gallicus*	brood/pupae	poss mis-id ***P.* dominula**	*Guiglia 1972 cited in* Makino 1985
9	Ichneumonidae	*Latibulus*	*nigrinotum*	*Polistes*	*snelleni*	brood/pupae		Kanai et al. 2001
				Polistes	*nipponensis*	brood/pupae		Kanai et al. 2001
				Polistes	*jadwigae*	brood/pupae		Oh et al. 2012
10	Ichneumonidae	*Pachysomoides*	*flavescens*	*Polistes*	*cubensis*	brood/pupae	syn. *Polistiphaga fulvescens*	Nelson 1968

Natural enemy				Hosts		Life stage attacked	Notes	Refs
Order	**Family**	**Genus**	**Species**	**Genus**	**Species**			
11	Ichneumonidae	*Pachysomoides*	*fulvus*	*Polistes*	*variatus*	brood/pupae	syn. *Polistiphaga fulva*	Rau 1941
				Polistes	*fuscatus*	brood/pupae	syn. *Polistiphaga fulva*	Rabb 1960
				Polistes	*annularis*	brood/pupae	syn. *Polistiphaga fulva*	Rau 1941
				Polistes	*pallipes*	brood/pupae	syn. *Polistiphaga fulva*	Rau 1941
				Polistes	*rubiginosis*	brood/pupae	syn. *Polistiphaga fulva*	Rau 1941
				Polistes	*exclamans*	brood/pupae	syn. *Polistiphaga fulva*	Rabb 1960; Strassmann 1981b
				Polistes	*apachus*	brood/pupae		Nelson 1968
				Polistes	*canadensis*	brood/pupae		Nelson 1968
				Polistes	*cubensis*	brood/pupae		Nelson 1968
				Polistes	*metricus*	brood/pupae		Nelson 1968
12	Ichneumonidae	*Pachysomoides*	*iheringa*	*Polistes*	*canadensis*	brood/pupae		Jeanne 1979
				Polistes	*versicolor*	brood/pupae		*Townes & Townes 1962 cited in* Makino 1985
13	Ichneumonidae	*Pachysomoides*	*stupidus*	*Polistes*	*exclamans*	brood/pupae		Strassmann 1981b
				Polistes	*annularis*	brood/pupae	syn. *Polistiphaga stupidus*	Rabb 1960
				Polistes	*erythrocephalus*	brood/pupae		Makino 1985
14	Ichneumonidae	*Pachysomoides*	*vespicola*	*Polistes*	*melasoma*	brood/pupae		*Townes & Townes 1962 cited in* Makino 1985
		Pachysomoides	*sp.*	*Polistes*	*satan*	brood/pupae		Kudô et al. 2013
Lepidoptera								
1	Crambidae	*Chalcoela*	*iphitalis*	*Polistes*	*exclamans*	brood/pupae	**40 - 73% brood destroyed**	Strassmann 1981a, 1981b; Rau 1941
				Polistes	*instabilis*	brood/pupae		Rau 1941
				Polistes	*carnifax*	brood/pupae		Rau 1941

Natural enemy				Hosts		Life stage attacked	Notes	Refs
Order	**Family**	**Genus**	**Species**	**Genus**	**Species**			
1 (cont.)	Crambidae	*Chalcoela*	*iphitalis*	*Polistes*	*major*	brood/pupae		Rau 1941
				Polistes	*metricus*	brood/pupae		Nelson 1968
				Polistes	*annularis*	brood/pupae		Nelson 1968
				Polistes	*fusactus*	brood/pupae		Nelson 1968
				Polistes	***dominula***	brood/pupae		Madden et al. 2010
				Polistes	*bellicosus*	brood/pupae		Nacko & Henderson 2017
				Polistes	*dorsalis*	brood/pupae		Nacko & Henderson 2017
2	Crambidae	*Chalcoela*	*pegasalis*	*Polistes*	*annularis*	brood/pupae	3 generations?	Rau 1941; Rabb 1960
				Polistes	*pallipes*	brood/pupae	**May have eliminated Polistes from islands in the West Indies**	Rau 1941
				Polistes	*variatus*	brood/pupae	syn *Dicymolomia pegasalis*	Rau 1941
				Polistes	*critinus*	brood/pupae	syn *Dicymolomia pegasalis*	Nelson 1968
				Polistes	*bellicosus*	brood/pupae	syn *Dicymolomia pegasalis*	Nelson 1968
				Polistes	*rubiginosus*	brood/pupae	syn *Dicymolomia pegasalis*	Rau 1941
				Polistes	*fuscatus*	brood/pupae	syn *Dicymolomia pegasalis*	Rabb 1960
				Polistes	*exclamans*	brood/pupae	syn *Dicymolomia pegasalis*	Rabb 1960
				Polistes	*metricus*	brood/pupae	syn *Dicymolomia pegasalis*	Nelson 1968
Strepsiptera								
1	Xenidae	*Xenos*	*afer*	*Polistes*	*marginalis*	brood - adult		Cook 2019
				Polistes	*tristis*	brood - adult		Cook 2019
				Polistes	*Africanus*	brood - adult		Cook 2019

Natural enemy				Hosts		Life stage attacked	Notes	Refs
Order	Family	Genus	Species	Genus	Species			
2	Xenidae	*Xenos*	*argentinus*	*Polistes*	*cavapyta*	brood - adult		Cook 2019
3	Xenidae	*Xenos*	*boharti*	*Polistes*	*peruvianus*	brood - adult		Cook 2019
4	Xenidae	*Xenos*	*bohlsi*	*Polistes*	*canadensis*	brood - adult		Cook 2019
5	Xenidae	*Xenos*	*bonariensis*	*Polistes*	*versicolor*	brood - adult		Cook 2019
6	Xenidae	*Xenos*	*circularis*	*Polistes*	*rothneyi gressitti*	brood - adult		Cook 2019
7	Xenidae	*Xenos*	*hamiltoni*	*Polistes*	*carnifax*	brood - adult		Cook 2019
8	Xenidae	*Xenos*	*hebraei*	*Polistes*	*olivaceus*	brood - adult		Cook 2019
9	Xenidae	*Xenos*	*hospitus*	*Polistes*	*versicolor*	brood - adult		Cook 2019
10	Xenidae	*Xenos*	*hunteri*	*Polistes*	*sp*	brood - adult		Cook 2019
11	Xenidae	*Xenos*	*indespectus*	*Polistes*	*sp*	brood - adult		Cook 2019
12	Xenidae	*Xenos*	*ivei*	*Polistes*	*critinus*	brood - adult		Cook 2019
13	Xenidae	*Xenos*	*kifunei*	*Polistes*	*comanchus navajoe*	brood - adult		Cook 2019
14	Xenidae	*Xenos*	*minor*	*Polistes*	*associus*	brood - adult		Cook 2019
				Polistes	*gallicus*	brood - adult		Cook 2019
15	Xenidae	*Xenos*	*niger*	*Polistes*	*tenellus*	brood - adult		Cook 2019
16	Xenidae	*Xenos*	*nigrescens*	*Polistes*	*carolina*	brood - adult		Cook 2019
17	Xenidae	*Xenos*	*pallidus*	*Polistes*	*annularis*	brood - adult		Cook 2019
				Polistes	*vellicosus*	brood - adult		Cook 2019
18	Xenidae	*Xenos*	*peckii*	*Polistes*	*metricus*	brood - adult	syn *P. metrica*	Hodges et al. 2003
				Polistes	*fuscatus*	brood - adult		Cook 2019
				Polistes	*apachus*	brood - adult		Cook 2019
				Polistes	*aurifer*	brood - adult		Cook 2019

Natural enemy				Hosts		Life stage attacked	Notes	Refs
Order	Family	Genus	Species	Genus	Species			
18 (cont.)	Xenidae	*Xenos*	*peckii*	*Polistes*	*flavus*	brood - adult		Cook 2019
				Polistes	*carolina*	brood - adult		Cook 2019
19	Xenidae	*Xenos*	*peruensis*	*Polistes*	*lanio*	brood - adult		Cook 2019
20	Xenidae	*Xenos*	*rostratus*	*Polistes*	*billardieri biglumoides*	brood - adult		Cook 2019
				Polistes	*billardieri ruficornis*	brood - adult		Cook 2019
21	Xenidae	*Xenos*	*rubiginosi*	*Polistes*	*carolina*	brood - adult		Cook 2019
22	Xenidae	*Xenos*	*stuckenbergi*	*Polistes*	*marginalis*	brood - adult		Cook 2019
23	Xenidae	*Xenos*	*vesparum*	*Polistes*	*biglumis*	brood - adult		Smit & Smit 2014
				Polistes	***dominula***	brood - adult		Hughes et al. 2003
				Polistes	*nimpha*	brood - adult		Smit & Smit 2014
				Polistes	*atrimandibularis*	brood - adult		Smit & Smit 2014
				Polistes	*semenowi*	brood - adult		Smit & Smit 2014
				Polistes	*gallicus*	brood - adult		Cook 2019
				Vespula	*vulgaris*	brood - adult		Cook 2019
24	Xenidae	*Xenos*	*yamaneorum*	*Polistes*	*gigas*	brood - adult		Cook 2019