INDIGENOUS WOODWASP (SIRICID SPP.) PARASITOID COMMUNITIES AND PRINCIPAL BIOLOGICAL CONTROL AGENTS OF SIREX NOCTILIO IN AUSTRALASIA: A REVIEW

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1. INTRODUCTION

The European woodwasp, *Sirex noctilio* F. (Hymenoptera: Siricidae), which is native to southern Europe, North Africa and southern parts of the Near East, first appeared as an exotic pest of pine plantations in Australasia in the early 1900s (Nutall, 1989). Since then, its worldwide range has expanded. The woodwasp invaded South America through Uruguay in 1980 and has now spread to Argentina (1985) and Brazil (1988) (Ciesla, 1993); it has also now invaded South Africa, entering via the Cape in 1994 (Tribe, 1994).

Soon after the woodwasp invaded Australasia a classical biological control project was set up between New Zealand and Australia. One of the main purposes of this project was to survey for and select host- or genus-specific parasitoids from the area of origin of the woodwasp. However, in addition to this, surveys were also undertaken on other, closely related pine-feeding woodwasps in other continents to establish the full range of potential agents available. Thus, the survey did not restrict itself to the 'old association' hypothesis which states that closely evolved natural enemies are likely to be the best control agents.

In view of the seriousness of the woodwasp in Brazil, Uruguay and also now in South Africa, classical biological control programmes are being set up in these countries to curb the spread of the woodwasp and reduce the damage being caused. Here I will summarise: the results of the surveys for natural enemies conducted for the Australasia project; the initial assessment of parasitoid species on *Sirex noctilio*; and those species found to be good biological control agents after release. Most of this information can be found in Taylor (1976).

2. SIRICID PARASITOID COMMUNITIES

In its native environment, the European woodwasp is not considered a serious pest. Thus when this species first invaded Australasia at the turn of the century, little was known about the ecology of this species or of closely related species. Likewise, little was known about the natural enemy communities associated with these insects (Berryman, 1986).

New Zealand was the first country to request parasitoids and between 1928 and 1952, two species (*Rhyssa persuasoria persuasoria* (L.) (Ichneumonidae) and *Ibalia leucospoides leucospoides* (Hochenworth) (Ibaliidae) were collected by the International Institute of Biological Control (IIBC, formerly CIBC) from *Sirex noctilio* in the UK and shipped to the Forest Research Institute in New Zealand (Nuttall, 1989).

After the discovery of the woodwasp in the state of Victoria in 1961, on the Australian mainland, a coordinated research programme was initiated in 1962 to search for and establish additional exotic natural enemies. Natural enemies in the European region, Turkey and North Africa were undertaken by staff of the CSIRO Division of Entomology. A Sirex Biological Control Unit was established at Silwood Park, Berkshire, U.K. for the study and quarantine of siricid woodwasps and their natural enemies (Taylor, 1976). Collection in other parts of the world were mostly undertaken by CSIRO and IIBC. Areas included: Himalayan regions, India and Pakistan, the USA (California, Nevada and the south-east), Canada (New Brunswick) and Japan. One collection was made in Canada (Vancouver) by Dr. B. P. Beirne (Taylor, 1976). All siricids and their natural enemies were also sent to the CSIRO laboratory at Silwood Park for study and shipment to Australia. In order to receive parasitoids, a Sirex unit was established at Hobart airport, Tasmania, where the species received could be reared and distributed to the Sirex infested areas in Australia; material for New Zealand was sent direct from Silwood Park, Tasmania or from IIBC stations. The search for natural enemies in the northern hemisphere was completed in 1972.

As mentioned earlier, the major aim of the surveys in the northern hemisphere was to collect all insect natural enemy species (including different populations of some species) associated with siricids in conifers from a wide range of climates (Taylor, 1976); particular attention was paid to Mediterranean-type climates (Kirk, 1974).

The results of the surveys are given in table 1. Here the species compositions of the communities in each of the regions are listed. It is likely that the number of species listed for each country/region is a function of sampling intensity and the size of the region sampled. The most common and important species in all communities are the ibaliids (Hymenoptera: Ibaliidae), which attack the eggs and early larval instars, and the ectoparasitic ichneumonids, *Rhyssa* spp and *Megarhyssa* spp. (Hymenoptera: Ichneumonidae), which attack the larger larvae. These two groups of parasitoids complement one another because they attack their hosts at different times during their development. It should be noted that *Ibalia ensiger* Norton is considered a subspecies of *I. leucospoides* Hochenw. and *I. drewseni* Borries a subspecies of *I. rufipes* Cresson (Kerrich, 1975). Finally, it is now known that *Megischus* sp. (Hymenoptera: Stephanidae) and *Pristaulacus ater* (Westwood) (Hymenoptera: Aulacidae) are probably not parasitic on siricids.

The siricid parasitoid communities in Europe, Turkey and North Africa have been particularly well studied (Spradbery and Kirk, 1978). The host siricids located with their individual parasitoid communities are shown in table 2 (modified from Spradbery and Kirk, 1978). Most of these siricids attack species of *Pinus, Picea, Larix, Cedrus* and *Abies*. It can be seen from table 2 that most of the parasitoids recorded are polyphagous but not all are parasitic on *Sirex noctilio*. The phenology of parasitoid attack on their hosts is as follows. *Ibalia leucospoides* emerges in the summer and autumn to attack *Sirex* larvae hatching soon after oviposition. However, *Ibalia rufipes drewseni* emerges in late spring to attack larvae in trees where the hatching has been delayed (Spradbery, 1970). All the other parasitoids attack later stages of the larvae. These species possess a long ovipositor which is inserted through the wood in order to reach the host.

The species within the parasitoid community on *Sirex noctilio* clearly coexist by exploiting different host stages or by having a temporal distribution pattern of attack. All species are widely distributed throughout the region where their host occurs and some species (e.g. *Rhyssa persuasoria* persuasoria) also have a more extensive range in view of their wide host range.

On the basis of the structure of the siricid parasitoid communities found in Europe and elsewhere, it was decided to try and establish host- or genus-specific early and late larval instar parasitoids.

3. ASSESSMENT OF POTENTIAL AGENTS ON Sirex noctilio

All assessments of parasitoids on *Sirex noctilio* from other siricid hosts were conducted at the *Sirex* units at Silwood Park, U.K. and Hobart, Tasmania (Taylor, 1976) and/or at the Forest Research Institute in New Zealand. A total of 21 species (including species collected from *Sirex noctilio*) were imported for assessment and rearing. Details of shipments and the numbers received are reviewed by Taylor (1976) and Nuttall (1989). Preliminary work (e.g. Spradbery and Kirk, 1978) showed that some parasitoid species are specific on host trees of genera other than *Pinus* and/or the other host siricids. Examples from Europe include *Megarhyssa emarginatoria* Thunberg and *Rhyssa amoena* Grav. Some other species of parasitoid were found to attack *Sirex noctilio* in the laboratory but cultures failed because of poor sex ratio problems. Examples here include *Rhyssa lineolata* (Kirby)and *Rhyssa alaskensis* (Ashmead).

As a result of these assessments on *Sirex noctilio*, ten principal species (with subspecies and geographic races) were reared in sufficient numbers for trial field releases (Table 3).

4. MAJOR BIOLOGICAL CONTROL AGENTS

The ten parasitoid species 'selected' as potential biological control agents were directly field released in Australia without further study; some of these species were also released in New Zealand. These releases have been extensively reviewed by Taylor (1976) and Nuttall (1989). Five of these species became established in the field in various parts of Australasia and these are summarised in Table 4.

Ibalia leucospoides (subspecies leucosopoides and ensiger) and Megarhyssa nortoni were the most rapid colonisers. Rhyssa was slow to colonise. Schlettererius cinctipes (Cresson) (Stephanidae) was rare in areas where the two ichneumonids were present. Ibalia species produce the highest levels of parasitism (14.5-28.9) in the Australian mainland, followed by Megarhyssa nortoni (12% or less); Rhyssa persuasoria failed to establish on the mainland. However, in Tasmania, Megarhyssa nortoni and Rhyssa persuasoria were the most abundant parasitoids. In New Zealand, parasitism by Ibalia I. leucospoides and the rhyssines has been 70% or more. Taylor (1967) provides a key to distinguish these biological control agents in the field.

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Table 1. Siricid parasitoid communities (modified from Taylor, 1976)

Country/region	Species
S.W. USA	Ibalia leucospoides ensiger Ibalia montana Ibalia ruficollis Ibalia rufipes rufipes Megarhyssa nortoni nortoni Rhyssa alaskensis Rhyssa hoferi Rhyssa persuasoria Schlettererius cinctipes
S.E. USA	Ibalia leucospoides ensiger Megischus sp. Pristaulacus ater Rhyssa howdenorum Rhyssa persuasoria persuasoria Rhyssa lineolata
E. Canada	Ibalia leucospoides ensiger Ibalia rufipes rufipes Megarhyssa nortoni quebecensis Rhyssa crevieri Rhyssa lineolata Rhyssa persuasoria persuasoria
W. Canada	Megarhyssa nortoni nortoni
Europe and Turkey	Ibalia leucospoides leucospoides Ibalia rufipes drewseni Megarhyssa emarginatoria Odontocolon geniculatus Rhyssa amoena Rhyssa persuasoria persuasoria
Morocco	Ibalia leucospoides leucospoides Rhyssa persuasoria persuasoria
India	Rhyssa persuasoria himalayensis
Japan	Ibalia aprilina Ibalia leucospoides leucospoides Megarhyssa praecellens Rhyssa jozana Rhyssa persuasoria persuasoria

Table 2. Host records of parasitoids of siricids (modified from Spradbery and Kirk, 1978)

				Host s	Host species			
Species	Sirex noctilo	S. cyaneus	S. juvencus	Urocerus	U. augur	U. sah	U. fantoma	Xeris
R.	+	+	+	- +	+	+	+	+
persuasoria								4
R. amoena	0	+	+	+	+	0		F -
M.	0	+	+	+	+	0	0	+
emarginatori								
a							-	
1.1.	+	+	+	+	+	+	+	ŀ
leucospoide								
S							0	
1. r.	+	+	+	+	+	>	>	ŀ
drewseni								
Ö.	+	+	+	+	+	0	>	
geniculatum								

Table 3. Principal species of siricid parasitoid reared in sufficient numbers for field release (see Taylor, 1976 for further details)

Species	Stage attacked	Origin
Ibalia leucospoides	Egg/ Young larvae	Europe
leucospoides		
Ibalia I. ensiger	u	USA
Ibalia rufipes rufipes	и	USA
Ibalia r. drewseni	и	Europe
Megarhyssa nortoni nortoni	Late larvae	USA
Megarhyssa praecellens	и	Japan
Rhyssa persuasoria persuasoria	4	Europe
Rhyssa p. himalayensis	at .	India
Rhyssa alaskensis	ű	USA
Rhyssa hoferi	u	USA
Rhyssa lineolata	ű.	Canada
Odontocolon geniculatus	<u>u</u>	Europe
Schlettererius cinctipes	Œ	USA

Table 4. Siricid parasitoid species established in the field in Australia and New Zealand (period 1929-1984)

Ibalia leucospoides leucospoides	
Ibalia I. ensiger	<u> </u>
Ibalia rufipes drewseni	
Megarhyssa nortoni nortoni	
Rhyssa persuasoria persuasoria	
Schlettererius cinctipes	