**Chapter 37**

***Sirex noctilio* Fabricius, (Hymenoptera: Symphyta)**

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# 37.1 Pest Status

*Sirex noctilio* Fabricius (Hymenoptera: Sumphyta) was first detected in Canada in 2005 (de Groot *et al.*, 2006), and subsequent surveys indicate that it is established in much of southern Ontario and a few locations in Quebec (Canadian Food Inspection Agency, 2008, see Fig 1. in Dodds *et al.*, 2010, L. Shields, where?, 2012, personal communication). Since its detection, there has been considerable debate about its potential impact in Canada. This debate stems from its pest status elsewhere; in its native range in Eurasia and Northern Africa the *S. noctilio* is typically a secondary pest of *Pinus* spp. (Pinaceae) and is of little economic concern (Wermelinger and Thomsen, 2012), whereas in other introduced regions it has had significant economic impact in introduced *Pinus* spp. plantations (Morgan and Stewart, 1966; Hurley *et al.*, 2007). Although Yemshanov *et al.* (2009) predict significant losses as a result of this insect, $86 to 254 million per year after 20 years, Dodds *et al.* (2010) note that *S. noctilio* is currently functioning somewhere between a primary and secondary pest in *Pinus* spp. stands in eastern North America.

*Sirex noctilio’s* complex life history allows it to kill trees. Unlike native woodwasps, *S. noctilio* attacks living trees; it favours stressed, suppressed and declining ones but also attacks and kills healthy hosts (Rawlings, 1948; Morgan and Stewart, 1966; Neumann *et al*., 1987). It has an obligate association with *Amylostereum areolatum* (Fries) Boiden (Russulales: Amylostereaceae), a white rot fungus, which the female carries and nurtures within internal storage organs (Gaut, 1969). The wasp also manufactures a phytotoxic mucus (Coutts and Dolezal, 1969). After the female *S. noctilio* oviposits into tunnels drilled into the sapwood of its host tree, it drills an adjacent tunnel and inoculates it with fragments of the fungal symbiont, along with the phytotoxin (Coutts, 1969a; Coutts and Dolezal, 1969). The fungus and mucus are thought to act in combination to cause physiological stress to the tree (Coutts, 1969a,b). These substances cause altered water balance within the needles, and impaired photosynthate translocation and respiration within the tree; tree death may follow (Coutts, 1969a; Fong and Crowden, 1973; Madden, 1977, Madden and Coutts, 1979). Symptoms of toxicity include foliar chlorosis, reddening and senescence, occurring as early as two weeks after *S. noctilio* attack (Coutts, 1969a; Ryan, 2011). *Sirex noctilio* favours *Pinus* spp. and most species are believed to be susceptible to the wasp (e.g. Morgan and Stewart 1966, Spradbery and Kirk 1978). In its current North American range, *S. noctilio* has successfully attacked and completed development in Scot’s pine, *Pinus sylvestris* L., red pine,*P. resinosa* Aiton, and Scot’s pine, *P. banksiana* (Lamb.) (Pinaceae) (Ryan *et al.*, 2011a) and evidence suggests it attacks white pine, *P. strobus* L. as well (K. Ryan, 2012, unpublished results). *Sirex noctilio* tends to show a higher oviposition density, produces more mucus, and manufactures a more potent phytotoxin than other woodwasp species, which allows it to kill trees (Spradbery, 1973, 1977).

In addition to assisting with overcoming tree defenses, the mucus and fungus are necessary for the development of *S. noctilio* offspring. The mucus facilitates *A. areolatum* growth in the host tree (Boros, 1968; Titze and Turnbull, 1970), and the fungus is essential for egg hatching and for larval development and nutrition (reviewed in Ryan and Hurley, 2012). Therefore when tree and climate conditions are favourable for fungal growth offspring are larger, and when environmental conditions are poor egg eclosion can be delayed or larvae may be small (Madden, 1981).

*Sirex noctilio* usually completes its lifecycle in one-year, although it can range from three months in very warm climates, to 2-3 years in cooler ones (Morgan, 1968; Neumann and Minko, 1981). Development time is related to both ambient temperature and wood moisture; models estimate that the wasp’s development requires 2500°d above a threshold of 6.8°C (Madden, 1981). This suggests that the wasp will have a development time of one year or more in Canada. Adults emerge between late-June and late-September in Ontario, with emergence peaking between mid-July and late-August (Ryan *et al.*, in press). The adult life-span is brief: males live up to 12 days and females up to 5 days (Neumann *et al*., 1987). Adults are sexually mature at emergence and do not feed, surviving on fat reserves (Taylor, 1981; Neumann *et al.*, 1987). Immediately after mating, females begin searching for suitable host trees. Unmated females show a similar host location response (Madden, 1988); *S. noctilio* is facultatively parthenogenetic with unfertilized eggs producing only males (Rawlings, 1953).

The potential fecundity of *S. noctilio* varies according to body size, ranging between 21 and 500 eggs per female (Madden, 1974; Zondag and Nuttall, 1977; Neumann *et al.*, 1987). Mean potential fecundity estimates of 264 and 212 eggs/female have been reported for populatins in Europe and Australia respectively (Spradbery, 1977; Neumann *et al.*, 1987). In Ontario, females appear to be smaller, and therefore less fecund (estimated average 111 eggs/female (K. Ryan 2012, unpublished results)]. Even in ideal conditions females only lay, on average, 82% of their egg complement, with smaller females laying an even smaller percentage (Neumann and Minko, 1981). Egg and early larval mortality can occur as a result of effective compartmentalization by the host tree or when growth of *A. areolatum* is lacking or insufficient (summarized in Neumann *et al.*, 1987). Because females are parthenogenetic, high male:female sex ratios can occur (Rawlings, 1953). When this happens, mate finding is difficult and the reproductive potential would be lowered (e.g., Zondag and Nuttall, 1977; Iede *et al.*, 1998; Hurley *et al.*, 2008).

Natural dispersal is estimated up to 30-50 km per year (Haugen *et al.*, 1990). Healthy *S. noctilio* females can fly an average of 30 km in 23 h on a flight mill (Villicide and Corley, 2008) and this fits with Haugen *et al.’s* (1990) dispersal estimate. Movement of infested material augments natural dispersal; life stages are reported to be resistant to wood drying and sometimes to chemical treatment (Haugen *et al.*, 1990). Woodwasps oviposit directly into the sapwood of the tree, thus, it can be difficult to determine if material is infested with immature stages of *S. noctilio*.

# 37.2 Background

The natural enemies of *S. noctilio* in its native Eurasian range include several hymenopteran parasitoid species, a parasitic nematode and birds (Bedding and Akhurst, 1978; Spradbery and Kirk, 1978; Spradbery, 1990). A cytoplasmic polyhedral virus has been identified in *S. noctilio* in Germany, however it remains unstudied (Talbot, 1977). Tree and stand conditions also have a strong influence on *S. noctilio* populations (e.g., Neumann *et al.*, 1987). In its present range in Canada, natural enemies currently function to limit *S. noctilio* populations and stand conditions can be expected to affect the wasp populations locally.

The most common hymenopteran species known to parasitize *S. noctilio* include *Ibalia* spp. (Hymenoptera: Ibaliidae), which attack eggs and early instar larvae, and *Rhyssa* and *Megarhyssa* spp. (Hymenoptera: Ichneumonidae), which parasitize later larval instars (Taylor, 1976). Parasitoid species, representing all three of these genera are present throughout Canada, including *S. noctilio’s* current range, where they parasitize native woodwasps (Table 1). In the woodwasp’s native range, *Rhyssa. persuasoria* (L.) (Hymenoptera: Ichneumonidae) and *Ibalia leucospoides leucospoides* (Hochenwarth) (Hymenoptera: Ibaliidae) account for the highest parasitism rates in the siricid community, 34% and 22% respectively (Spradbery and Kirk, 1978). *Ibalia leucospoides* is abundant in *S. noctilio*-infested trees in Ontario, accounting for a mean hypothetical parasitism rate of 19.8% in 60 trees; *Rhyssa lineolata* (Kirby) and *R. persuasoria* (L.) (Hymenoptera: Ichneumonidae) account for a further 2.2 and 1.4% respectively (Ryan *et al.*, in press). In the conterminous United States Long *et al.* (2009) report similar parasitism by *I. leucospoides* (20.5% per tree), and *R. lineolata* and *Megarhyssa nortoni* (Cresson) (Hymenoptera: Ichneumonidae) collectively account for a further 1.3% per tree. In Ontario, parasitism by *I. leucospoides* is generally uniform between tree species, stands and years, therefore, is expected to provide consistent population control (Ryan *et al.*, in press).

The infective stage of the nematode *Deladenus* (*Beddingia*) *siricidicola* Bedding (Tylenchida: Neotylenchidae) parasitizes *S. noctilio* eggs, sterilizing the adult females (Bedding, 1968, 1972; Bedding and Akhurst, 1978). *Deladenus siricidicola* has two separate life cycles, a free-living fungus feeding cycle and a parasitic cycle. The mycetophagous form of *D. siricidicola* lives in the tracheids and resin canals of the tree, feeding on *S. noctilio’s* fungal symbiont *A. areolatum*; the parasitic form emerges when *S. noctilio* larvae are present (Bedding, 1972). A female *D. siricidicola* of the parasitic form breaches the woodwasp’s larval integument and when the nematode strain is compatible with the woodwasp species and strain, the offspring of the infective female nematode enter the reproductive organs of the wasp just before the end of its pupation (Bedding, 1972). When *S. noctilio* females are parasitized, ovary and egg development are suppressed and the remaining eggs contain juvenile nematodes that are introduced into the tree when the woodwasp attempts to oviposit. *Deladenus siricidicola* has been the focus of most of the classical biological control efforts throughout the introduced range of the wasp in the southern hemisphere, some of which have been highly successful (reviewed in Hurley *et al.*, 2007). However, the infection rate and function of this natural enemy in *S. noctilio* populations in the wasp’s native range are undescribed. *Deladenus siricidicola* is prevalent in *S. noctilio* in Canada, being found in 38% of 1445 females wasps, however, it is found in the haemocoel or the egg sheaths of the wasp rather than the eggs so it is unlikely to cause sterilization (Yu *et al*., 2009, Ryan *et al.*, in press). Williams *et al*. (2012) hypothesized that the reason why *S. noctilio* eggs were not sterilized by the nematode strain present in North America is because of the presence of a developmental asynchrony between the two organisms; the sterilizing *D. siricidicola* juveniles may emerge too late, the woodwasps egg sheath having hardened and become impenetrable (Williams *et al.*, 2012). The “North American” nematode strain could function as a sub-lethal natural enemy if the presence of the nematode in the wasp’s haemocoel affects the performance of female *S. noctilio*. Nematode-sterilized *S. noctilio* females are often smaller and have reduced fat bodies (Bedding, 1972; Villicide and Corley, 2008). Since body size is correlated with fecundity (Madden, 1974), and smaller females have less dispersal capacity (Villicide and Corley, 2008), non-sterilizing nematode infection could still have a negative effect on *S. noctilio* populations if they caused a similar difference in body size.

Bird predation augments *S. noctilio* mortality caused by invertebrate natural enemies; woodpeckers (Piciformes: Picidae), attack larval woodwasps within the sapwood and aerial predators attack the flying adults. Predation by woodpeckers in the wasp’s native range is estimated to account for 6% larval mortality (Spradbery, 1990). Aerial predators are reported to attack mating swarms where they feed on the adult *S. noctilio* as well as disrupt mating, resulting in higher male:female ratios in subsequent years (Madden, 1982). Although there has been no investigation of bird predation in Canada, these predators are expected to be part of the natural enemy complex here. Woodpecker activity, often extensive, is seen in *S. noctilio*-infested trees (K. Ryan, 2012, unpublished results).

*Sirex noctilio* favours trees that are suppressed, or physiologically stressed by drought, nutritional deprivation, pathogens, or other insect pests (e.g. Neumann *et al.*, 1987). Poor silviculture, resulting in overstocking and thus an abundance of suppressed and stressed trees in a stand, is cited as a main factor in outbreaks, (Neumann *et al.*, 1987; Madden, 1988; Dodds *et al.*, 2010). *Sirex noctilio* can also exploit short-term stressors including mechanical damage during management operations, weather-event related tree injury, herbicide use, cone harvesting or stand thinning, especially when these events occur during the insect’s flight season (summarized in Madden, 1988). An abundance of *S. noctilio*-favourable trees in a stand can lead to a local build-up in woodwasp populations; the wasps subsequently attack healthy trees, severely stressing them and predisposing them to future attack (Madden, 1968, 1975). Silvicultural management recommendations to maintain *S. noctilio* at endemic levels include: appropriate site selection for planting; timely thinning to maintain optimal stocking density, with removal of suppressed, deformed, diseased or dying trees; thinning outside of the insects flight season (i.e. in late fall and winter); minimizing tree injury; and early salvage of trees damaged by thinning or natural causes (Neumann *et al.*, 1987; Madden, 1988; Dodds *et al.*, 2010).

# 37.3 Biological Control Agents

To date, research about *S. noctilio* in Canada has focussed on examining the community of natural enemies and competitors of *S. noctilio* already present in its Canadian range, and on determining to what degree these organisms function to limit the woodwasp’s population (e.g., Yu *et al.*, 2009; Ryan *et al.*, 2011a; Ryan *et al.*, in press). As described in the previous section, there is strong evidence that both ibaliid (egg) and rhyssine (larval) parasitoids are currently parasitizing *S. noctilio* in its present range in Ontario and New York State, and *I. leucospoides* appears to be the woodwasp’s primary natural enemy (Ryan *et al.*, in press). There is also evidence that subcortical beetles interact with the wasp, and have a negative effect on *S. noctilio* populations (Ryan *et al.*, 2011a). These interactions may be mediated, at least in part, by the fungal associates of the insects; some beetle-vectored species of blue stain fungus, e.g., *Grosmannia clavigera* (Robinson-Jeffrey & R.W. Davidson) (Ophiostomatales: Ophiostomataceae), outcompete *S. noctilio’s* fungal symbiont, and there is evidence that the presence of these blue stain species deter *S. noctilio* oviposition activity (Ryan *et al.*,2011b, c). The effect of non-sterilizing nematodes on *S. noctilio* is less clear, and research has been initiated to begin to address this question. The development of PCR-RFLP methods for distinguishing *D. siricidicola* isolates in North America has recently been completed.

*Deladenus siricidicola* has been, and continues to be, the central focus of classical biological control efforts conducted in most of the woodwasp’s introduced range in the southern hemisphere (Bedding, 1993; Hurley *et al.*, 2007; Slippers *et al.*, 2012). Soon after the discovery of *S. noctilio* in North America, *D. siricidicola* was considered as a biological control option in the USA as well (Williams *et al.*, 2012). The mycetophagous life-cycle of *D. siricidicola* facilitates its mass production as a biological control agent since it can persist in this cycle in culture for several generations (Bedding, 1993). Results are highly successful in some regions (e.g. 75% to close to 100% infection in Australasia) but control with the nematode is poor in other areas (e.g., KwaZulu-Natal, South Africa <10%) (reviewed in Hurley *et al.*, 2007). Wood moisture is thought to be a key factor inhibiting infection, and this is influenced by climate; KwaZulu-Natal receives most of its precipitation in the summer unlike Australasia, where the methodology was developed, which receives more precipitation in the winter (Hurley *et al.*, 2008; Slippers *et al.*, 2012). Soon after the discovery of *S. noctilio* in New York State in 2004, and prior to the discovery of the presence of the “North American” nematode strain, controlled release experiments with *D. siricidicola* began in the USA (Williams and Mastro, 2008). Early investigators assumed that it would be relatively simple to adapt the techniques developed in Australasia to North America (Williams *et al.*, 2012). However, climatic differences affecting the timing of *D. siricidicola* application, the potential for non-target effects on native woodwasps and other woodboring insects, as well as competition or hybridization with the “North American” nematode strain are areas for further investigation before releases can be made (Williams *et al.,* 2012).

# 37.4 Evaluation of Biological Control

To date, no biological control agents have been released for *S. noctilio* in Canada.

# 37.5 Future Needs

Future work should include:

1. developing more effective sampling and survey tools and methods to continue monitoring of populations and for range extensions;
2. confirming the ubiquity and impact of *S. noctilio* parasitoids and parasites in Canada to better assess their potential for biological control;
3. investigating why strain(s) of *D. siricidicola* present in North America do(es) not sterilize *S. noctilio* eggs to inform future research about nematode biological control should it become necessary;
4. investigating *D. siricidicola* sterilization rates in Eurasia to clarify the need for the nematode to function as a sterilizing agent in North America;
5. determining how subcortical insect competition affects *S. noctilio* populations may elucidate further management options and could result in novel pest management options;
6. investigating overwintering mortality of *S. noctilio* and its invertebrate natural enemies, as well the effect of natural, fluctuating, temperature conditions on the wasp’s development, in order to forecast population density and thus the need for biological control in new ranges or changing climate conditions;
7. vigilance against further introductions because they may result in introductions of more vigorous strains of *A. areolatum* and consequently bigger wasps with greater reproductive abilities, thus affecting its future pest status.

# 37.6 References

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**Table 1.** Hymenoptera parasitoids of *Sirex noctilio* known from North America and Eurasia (Data from: Cameron, 1965; Taylor, 1976).

|  |  |
| --- | --- |
| **Region** | **Species** |
| Trans-Canada | *Ibalia leucospoides ensiger* Norton |
|  | *Pseudorhyssa ruficoxis* (Kriechbaumer) |
|  | *Rhyssa lineolata* (Kirby) |
|  | *Rhyssa persuasoria persuasoria* (L.) |
|  |  |
| Eastern Canada | *Ibalia leucospoides ensiger* Norton |
|  | *Ibalia montana* Cresson |
|  | *Ibalia rufipes rufipes* Cresson |
|  | *Megarhyssa nortoni quebecensis* (Provancher) |
|  | *Rhyssa crevieri* (Provancher) |
|  |  |
| Western Canada | *Ibalia montana* Cresson |
|  | *Megarhyssa nortoni nortoni* (Cresson) |
|  | *Rhyssa alaskensis* Ashmead |
|  |  |
| United States | *Ibalia leucospoides ensiger* Norton |
|  | *Ibalia montana* Cresson |
|  | *Ibalia ruficollis* Cameron |
|  | *Ibalia rufipes rufipes* Cresson |
|  | *Megarhyssa nortoni nortoni* (Cresson) |
|  | *Megarhyssa nortoni quebecensis* (Provancher) |
|  | *Megischus* sp. |
|  | *Pristaulacus niger (ater)* (Schukard) |
|  | *Rhyssa alaskensis* Ashmead |
|  | *Rhyssa crevieri* (Provancher) |
|  | *Rhyssa hoferi* Rohwer |
|  | *Rhyssa howdenorum* Townes |
|  | *Rhyssa lineolata* Kirby |
|  | *Rhyssa persuasoria persuasoria* (L.) |
|  | *Schlettererius cinctipes* (Cresson) |
|  |  |
| Eurasia & Northern Africa | *Ibalia jakowlewi* Jacobson |
|  | *Ibalia leucospoides leucospoides* (Hochewarth) |
|  | *Ibalia rufipes drewseni* Borries |
|  | *Megarhyssa emarginatoria* (Thunberg) |
|  | *Odontocolon geniculatum* (Kriechbaumer) |
|  | *Rhyssa amoena* (Gravenhorst) |
|  | *Rhyssa persuasoria persuasoria* (L.) |

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Trans Canada** | **Western Canada** | **Eastern Canada** | **USA** | **Eurasia & Northern Africa** |
| Aulacidae  *Pristaulacus niger (ater)* (Schukard) |  |  |  | X |  |
| Ichneumonidae  *Ibalia jakowlewi* Jacobson |  |  |  |  | X |
| *Ibalia leucospoides ensiger* Norton | X |  | X | X | X |
| *Ibalia leucospoides leucospoides* (Hochewarth) |  |  |  |  | X |
| *Ibalia montana* Cresson |  | X | X | X |  |
| *Ibalia ruficollis* Cameron |  |  |  | X |  |
| *Ibalia rufipes drewseni* Borries |  |  |  |  | X |
| *Ibalia rufipes rufipes* Cresson |  |  | X | X |  |
| *Megarhyssa emarginatoria* (Thunberg) |  |  |  |  | X |
| *Megarhyssa nortoni nortoni* (Cresson) |  | X |  | X |  |
| *Megarhyssa nortoni quebecensis* (Provancher) |  |  | X | X |  |
| *Odontocolon geniculatum* (Kriechbaumer) |  |  |  |  | X |
| *Pseudorhyssa ruficoxis* (Kriechbaumer) | X |  |  |  |  |
| *Rhyssa alaskensis* Ashmead |  | X |  | X |  |
| *Rhyssa amoena* (Gravenhorst) |  |  |  |  | X |
| *Rhyssa crevieri* (Provancher) |  |  | X | X |  |
| *Rhyssa hoferi* Rohwer |  |  |  | X |  |
| *Rhyssa howdenorum* Townes |  |  |  | X |  |
| *Rhyssa lineolata* (Kirby) | X |  |  | X |  |
| *Rhyssa persuasoria persuasoria* (L.) | X |  |  |  |  |
| Stephanidae  *Megischus* sp. |  |  |  | X |  |
| *Schlettererius cinctipes* (Cresson) |  |  |  | X |  |