Sirex species (Hymenoptera: Siricidae) and their parasitoids in *Pinus sylvestris* in eastern North America

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Abstract—Siricids and their parasitoids were reared from Scots pine (*Pinus sylvestris* L. (Pinaceae)) trees infested by *Sirex noctilio* F. in central New York State. *Sirex noctilio* accounted for 94.3% of the siricid specimens emerging, totaling 1313 specimens from six trees, with a maximum of 495 from one tree. Of the individuals emerging per tree, 20.6 ± 5.2% were female. Two native siricids, *Sirex nigricornis* F. and *S. edwardsii* Brullé, also emerged from trees but in low numbers. Three hymenopteran parasitoid species that attack siricids emerged, totaling 21.8 ± 6.4% parasitism per tree. *Ibalia leucospoides ensiger* Norton (Ibaliidae) was by far the most abundant parasitoid, at 20.5 ± 6.3% parasitism per tree. The percentage of female *S. noctilio* emerging was positively correlated with wood diameter, whereas percent parasitism by *I. l. ensiger* was negatively correlated with wood diameter.

Résumé—Des siricides et leurs parasitoïdes ont été élevés à partir de pin sylvestre, *Pinus sylvestris* L. (Pinaceae), infestés par *Sirex noctilio* F. collectés dans le centre de l'état de New York. *Sirex noctilio* représentait 94,3 % des siricides émergés de six arbres, soit un total de 1313 spécimens, avec un maximum de 495 *S. noctilio* pour un seul arbre. Parmi les *S. noctilio* émergés, 20,6 ± 5,2 % étaient des femelles. Deux siricides natifs (*Sirex nigricornis* F. et *S. edwardsii* Brullé) ont également émergé des arbres, mais toujours en petit nombre. Trois hyménoptères parasitoïdes s'attaquant aux siricides émergèrent également, pour un taux de parasitisme global de 21,8 ± 6,4 % par arbre. *Ibalia leucospoides ensiger* Norton (Ibaliidae) était de loin le parasitoïde le plus abondant avec un taux de parasitisme moyen par arbre de 20,5 ± 6,3 %. Le pourcentage de femelles *S. noctilio* émergeant était positivement corrélé avec le diamètre du bois, tandis que le taux de parasitisme par *I. l. ensiger* était négativement corrélé avec le diamètre du bois.

The wood wasp *Sirex noctilio* F. (Hymenoptera: Siricidae) is native to Eurasia (Spradbery and Kirk 1978) but has been introduced accidentally to numerous countries in the Southern Hemisphere (Hurley *et al.* 2007). In North America, *S. noctilio* was first collected in New York State in 2004 (Hoebeke *et al.* 2005) and Ontario, Canada, in 2005 (de Groot 2007). In the United States of America, *S. noctilio* had been reported from 29 counties in New York State, 7 counties in Pennsylvania, 4 counties in Michigan, and 1 county in Vermont by 2008 (National Agricultural Pest Information System (NAPIS) 2008).

In Southern Hemisphere countries where *S. noctilio* has been introduced, it has become a pest in commercial pine plantations by infesting and eventually killing pines (*Pinus* L. (Pinaceae)).

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Adult females inject a phytotoxic mucus and a symbiotic white rot fungus, *Amylostereum areolatum* (Fr.) Boidin, into trees when laying eggs; the mucus and fungus together kill the trees (Talbot 1977). Pines and *Sirex* spp. are not native to the Southern Hemisphere, and classical biological control programs have been widely used to introduce parasitic nematodes and hymenopteran parasitoids for control in *S. noctilio* (Hurley *et al.* 2007). These natural enemies were always collected from areas in the Palearctic and Nearctic regions where *S. noctilio* or other *Sirex* species are native.

Sirex noctilio, native North American species of *Sirex* L., and hymenopteran parasitoids (Ichneumonidae and Ibaliidae) were studied in central New York State using naturally infested pine trees harvested in 2007. We investigated the species of hymenopteran parasitoids associated with *Sirex* species and explored the relationship between wood diameter and the abundance of *S. noctilio* and the most commonly occurring parasitoid, *Ibalia leucospoides ensiger* Norton (Ibaliidae).

Six naturally infested Scots pine, *Pinus sylvestris* L., trees were sampled in late June 2007 at two sites in central New York State known to host populations of *S. noctilio*; in 2006 many trees at both sites exhibited symptoms of heavy attack (*i.e.*, resin beads) and at one site an average of >40 *S. noctilio* emerged from 2.1 m long sections of 30 infested trees (D.W. Williams, unpublished data). Four trees were felled in New Haven (43.47868°N, 76.35241°W) and two in Pompey (42.96212°N, 75.95803°W). For five trees, at least the lowest 1 m of each tree was not used, and for the additional tree, the lowest sample began 0.35 m above the ground; sampling was not designed to evaluate vertical distribution. Few insects emerged from one tree felled in Pompey from which wood samples with a total length of 150.5 cm and an average diameter of 13.2 ± 0.1 cm (mean ± SE) were obtained; these samples were not included in analyses of the association of emergence with wood diameter. The minimum diameter of wood used from the other trees was 6.1 ± 1.2 cm and the maximum diameter 17.3 ± 3.3 cm; the difference from smallest to largest diameter wood from a single tree was 11.2 ± 2.2 cm. The total length of wood from each of these trees was 10.0 ± 1.1 m. Wood was cut into bolts 50.2 ± 0.4 cm (mean ± SE) long and held at ambient temperature (18–30 °C) in cardboard barrels (69 cm height × 48 cm diameter) with screen lids. A contiguous section of a tree was placed in each barrel for rearing insects, with 5.2 ± 0.5 bolts/barrel (volume of wood/barrel = 2.95 ± 0.70 m^3), leaving space between bolts to allow insect emergence. From 2 July to 27 September 2007, all emerging *Sirex* spp. and parasitoids were collected every 1–3 days for indentification. No more insects emerged and, on 27 October, the study was discontinued. The wood was not dissected to detect any remaining living or dead insects, so the total number of insects in the wood samples could have been underestimated. Voucher specimens of each *Sirex* and parasitoid species have been deposited in the Cornell University Insect Collection (Lot Number 1264).

The association between the average diameter of wood in a barrel and total number of adult *S. noctilio*/m^3 (both male and female) was analyzed by logistic regression using a Poisson distribution (Proc Genmod; SAS Institute Inc. 2007). To analyze the association between wood diameter and percent female *S. noctilio* or percent parasitism by *I. l. ensiger*, random intercept mixed models with trees as a random effect were used with arcsine square root transformed proportion of female S. noctilio or proportion of parasitism by *I. l. ensiger* (Proc Mixed; SAS Institute Inc. 2007).

Sirex noctilio emerged from wood in every barrel and accounted for 94.3% of the siricid specimens collected, totaling 1313 specimens from all samples (Table 1). Nearly two-thirds (66.1%) of *S. noctilio* emerged from wood with a diameter ≤12.3 cm. Of these specimens, 20.6 ± 5.2% were female. Two native siricid species, *S. nigricornis* F. and *S. edwardsii* Brullé, also emerged from the same sections of the same trees as *S. noctilio*. This was somewhat surprising because both of these natives are known to carry the symbiotic fungus *Amylostereum chailletii* (Fr.) Boidin, whereas *S. noctilio* carries *A. areolatum* (Bedding and Akhurst 1978), and these fungal species are vegetatively incompatible (Thomsen and Koch 1999). Almost all *S. noctilio* (96.0%) emerged 8 days before either *S. nigricornis* or *S. edwardsii*. Most of the native *Sirex* (98.4% and 88.9% for *S. nigricornis* and *S. edwardsii*, respectively) emerged from wood with diameters ranging from 13.5 to 18.0 cm.

Three species of parasitoids emerged from *Sirex*-infested trees: two ichneumonids and one ibaliid (Table 2). The ibaliid (*I. l. ensiger*) accounted for 96.1% of all parasitoid specimens (91.7 ± 45.1 *I. l. ensiger* individuals/tree (mean ±

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Table 1. Three *Sirex* species that emerged from six Scots pine (*Pinus sylvestris*) trees in central New York State in 2007.

	No./tree	Percentage of females/tree*	No. of trees infested
S. noctilio	218.8 (64.9)	20.6 (5.2)	6
S. nigricornis	10.2 (8.0)	58.9 (16.1)	2
S. edwardsii	3.0 (2.4)	6.7 (6.7)	3

Note: Values are shown as the mean with SE in parentheses.
*Means were calculated using trees in which the species was present.

Table 2. Three parasitoid species associated with *Sirex* spp. emerging from six *Pinus sylvestris* trees in central New York State in 2007.

	No./tree	Percent parasitism/tree*	Percentage of females/tree†	No. of trees present
Ibalia leucospoides ensiger	91.7 (45.1)	20.5 (6.3)	45.7 (9.7)	5
Rhyssa lineolata	2.5 (1.2)	0.8 (0.5)	62.5 (37.5)	4
Megarhyssa nortoni	1.2 (0.7)	0.5 (0.3)	62.4 (9.0)	3

Note: Values are shown as the mean with SE in parentheses.
*Calculated as combined parasitism of *S. noctilio, S. nigricornis*, and *S. edwardsii*.
†Means were calculated using trees in which the species was present.

SE)) emerging from five of the six trees. The two ichneumonids, *Rhyssa lineolata* (Kirby) and *Megarhyssa nortoni* (Cresson), emerged from only four and three trees, respectively, with a maximum of seven and three individuals per tree, respectively. Both ichneumonid species emerged from both sites. In one section of one tree, both *I. l. ensiger* and *R. lineolata* emerged along with *S. noctilio* and both native siricids. *Megarhyssa nortoni* did not emerge from the same tree sections as the native siricids, though *M. nortoni* emerged from one of the trees from which *S. edwardsii* emerged. Because all three *Sirex* species emerged from the trees that were sampled, it is not possible to calculate percent parasitism for each *Sirex* species separately. Parasitism of *Sirex* spp. by all parasitoids was 21.8 ± 6.4% per tree.

No relationship was found between the total density of *S. noctilio* and the average diameter of wood. However, a significantly larger percentage of female *S. noctilio* emerged with increasing wood diameter (arcsine square root (proportion of females) = –0.04408 + 0.04748 × wood diameter; $F_{1,16.7}$ = 6.59, P = 0.0202) (Fig. 1). The inverse relationship was found for percent parasitism by *I. l. ensiger*, with fewer parasitoids emerging as wood diameter increased (arcsine square root (proportion of parasitism) = 0.9975 – 0.03981 × wood diameter; $F_{1,16}$ = 8.01, P = 0.0121) (Fig. 1).

The parasitoids reared in this study could have parasitized any of the three siricid species reared, but we hypothesize that much of the parasitism likely occurred on *S. noctilio*. Our study sites were 27.5 and 54.0 km from the site where *S. noctilio* was first detected in 2004, and *S. noctilio* has been found killing pines at these study sites since 2006 (D.W. Williams, unpublished data). Although the parasitoids reared in this study are Nearctic natives and *S. noctilio* is native to the Palearctic Region, parasitoids associated with concealed hosts frequently have broad host ranges (Strand 1986). In fact, two of the three parasitoid species that emerged in this study have previously been used for classical biological control of *S. noctilio* in the Southern Hemisphere (Hurley *et al.* 2007), and all three species have been recorded parasitizing numerous siricid species (Krombein *et al.* 1979). In our study, *I. l. ensiger*, which parasitizes eggs and younger larvae (Murphy 1998), was much more abundant than the two rhyssine ichneumonids (*M. nortoni* and *R. lineolata*), which attack later instars (Murphy 1998). In contrast, in Tasmania, parasitism of *S. noctilio* by rhyssines was much more common than parasitism by *I. leucospoides* (Taylor 1978).

Chiarello Penteado *et al.* (2000) showed that most *S. noctilio* and most *I. leucospoides* in Brazil emerged from the central 50% of trees, based on tree diameter. Our results showed that

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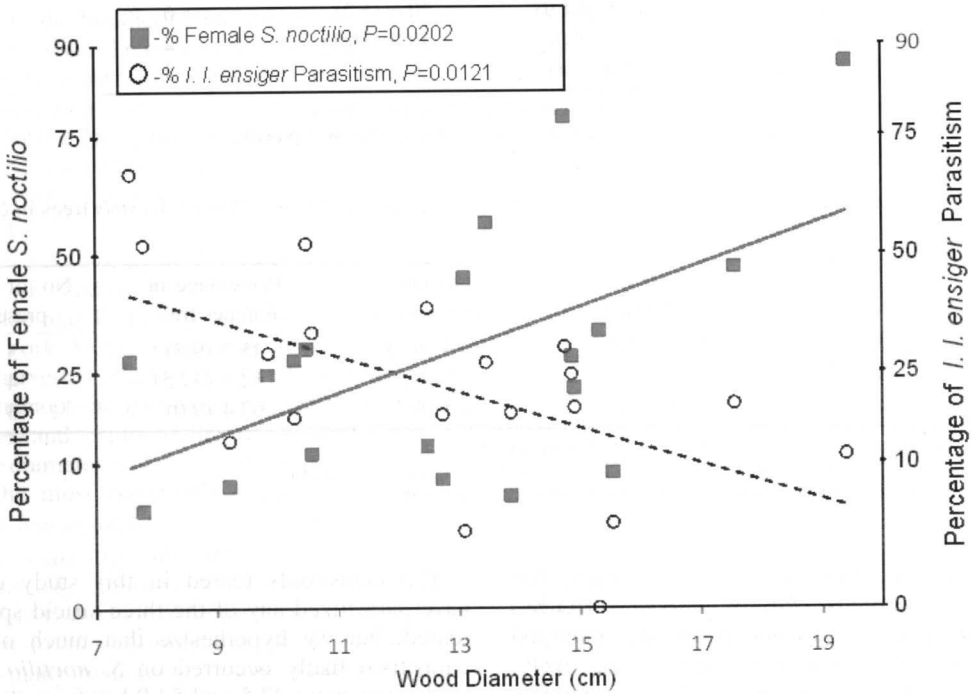
Fig. 1. Percentage of female *Sirex noctilio* (solid line) and percent parasitism by *Ibalia leucospoides ensiger* (dashed line) emerging from tree sections of various diameters; lines were calculated using arcsine square root transformed proportions. Only 10 male *S. noctilio* and no parasitoids emerged from wood samples totaling 150.5 cm in length from one tree in Pompey, New York; samples from this tree were not included in statistical analyses.



although the total number of *S. noctilio* emerging did not vary with tree diameter, the percentage of females increased significantly with tree diameter, which is similar to observations of Morgan and Stewart (1966) and Hurley *et al.* (2008). In contrast, the percentage of hosts parasitized by *I. l. ensiger* decreased significantly as tree diameter increased. This allocation of a greater percentage of female *S. noctilio* to larger diameter sections of the tree could allow female offspring to escape parasitism by *I. l. ensiger*. We hypothesize that oviposition by *I. l. ensiger* could be limited by some feature of larger diameter wood (*e.g.*, bark thickness) or by height in the tree, but these factors require further investigation.

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