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Author(s): K. Ryan, P. De Groot, R. W. Nott, S. Drabble, I. Ochoa, C. Davis, S. M. Smith, and J. J. Turgeon

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Natural Enemies Associated With *Sirex noctilio* (Hymenoptera: Siricidae) and *S. nigricornis* in Ontario, Canada

K. RYAN,^{1,2} P. DE GROOT,^{1,3,5} R. W. NOTT,³ S. DRABBLE,⁴ I. OCHOA,³ C. DAVIS,³ S. M. SMITH,¹
AND J. J. TURGEON³

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ABSTRACT *Sirex noctilio* F. is an exotic woodwasp now found in eastern North America where it shares natural enemies with native woodwasps of *Pinus* spp. To study the extent to which native hymenopteran parasitoids and parasitic nematodes could affect woodwasp populations, 60 *Pinus* trees with symptoms of *S. noctilio* attack were felled in 2007 and 2008 in Ontario, Canada. Each tree bole was cut into 1-m sections that were placed in individual rearing tubes; emergence was monitored from May to November of the year of felling. Female *S. noctilio* were dissected to assess parasitism by the nematode *Deladenus siricidicola* Bedding. Two species of Siricidae emerged from these trees; *S. noctilio*, which accounted for most of the specimens collected, and *S. nigricornis* F. Of the three species of parasitoid that emerged, *Ibalia leucospoides* (Hochenwarth) was the most abundant, accounting for an overall hypothetical Siricidae parasitism rate of almost 20%. This parasitoid emerged over a similar time period as *S. noctilio*—between early July and early September. Except in trees >15 m in height, parasitism by *I. leucospoides* generally appeared uniform throughout the bole. Parasitism rates did not vary between the 2 yr, but did between sites in 1 yr. Parasitic nematodes were found in the haemocoel of about one third of *S. noctilio* females dissected but were never found sterilizing the eggs; none were found in *S. noctilio* emerging from *P. resinosa*. These findings suggest that *I. leucospoides* is currently the primary invertebrate natural enemy of *S. noctilio* in Ontario.

KEY WORDS *Ibalia leucospoides*, *Deladenus siricidicola*, parasitoids, parasitic nematode, natural enemies

An established population of *Sirex noctilio* F. (Hymenoptera: Siricidae) was recently detected in north-eastern North America (Hoebeker et al. 2005, de Groot et al. 2006). To date, its distribution in Canada had been confirmed in Ontario and Quebec, and in the United States of America in New York, Pennsylvania, Michigan, Vermont, Ohio, and Connecticut (CFIA 2008, APHIS 2011). In its native range, Eurasia and northern Africa, *S. noctilio* is a secondary species of native *Pinus* spp. (Pinaceae) that has many natural enemies (e.g., hymenopteran parasitoids, a parasitic nematode, and avian predators [Bedding and Akhurst 1978, Spradbery and Kirk 1978, Madden 1982, Spradbery 1990]), and may compete with several species of bark beetles and woodborers for resources. In the areas of the southern hemisphere that *S. noctilio* has invaded, it has been an important pest of exotic *Pinus* spp. (Rawlings 1948, Neumann et al. 1987). In these areas of introduction the wasp occasionally invaded with one of its natural enemies (e.g., Zondag 1979, Filho et al. 1998), however, natural enemies typically have been absent until the implementation of classical

biological control programs (reviewed in Hurley et al. 2007). Knowledge of the type of interactions between *S. noctilio* and its community of natural enemies and competitors in Ontario is needed to better understand how this insect will behave in, and could impact North America's forests.

Hymenopteran species known to parasitize *S. noctilio* include *Ibalia* spp. (Ibaliidae), which attack eggs and first or second instars, and *Rhyssa* and *Megarhyssa* spp. (Ichneumonidae), which parasitize later instars (Morgan and Stewart 1966a, Taylor 1978). Another natural enemy of *S. noctilio* is the infective stage of the nematode *Deladenus siricidicola* Bedding (Neotylenchidae), which typically parasitizes *S. noctilio* eggs, sterilizing the adult female insect (Bedding 1968, 1972). This parasitic nematode has been the focus of most of the classical biological control efforts in much of the southern hemisphere, some of which have been highly successful (reviewed in Hurley et al. 2007).

Most of the hymenopteran parasitoids introduced into *S. noctilio* populations in the southern hemisphere are also native to North America (e.g., Cameron 1965, Murphy 1998, Cameron 2012). In eastern North America, *S. noctilio* is parasitized by *D. siricidicola* (Yu et al. 2009) and, it has been hypothesized that it is currently parasitized by *Ibalia leucospoides* (Hochenwarth), *Rhyssa lineolata* (Kirby),

¹ University of Toronto, Toronto, ON, M5S 3B3, Canada.

² Corresponding author, e-mail: kathleen.ryan@utoronto.ca.

³ Canadian Forest Service, Sault Ste. Marie, ON, P6A 2E5, Canada.

⁴ Ontario Tree Seed Plant, Angus, ON, L0M 1B0, Canada.

⁵ Deceased.

and *Megarhyssa nortoni* (Cresson) (Long et al. 2009), and could be by the species *I. rufipes rufipes* Cresson, *R. crevieri* (Provancher), and *R. persuasoria persuasoria* (L.) as well (Taylor 1976). Parasitism by these species is hypothetical as the parasitoid species were not reared directly from *S. noctilio* life stages, and may have emerged from other hosts colonizing the same tree. This hypothetical percentage of parasitism by hymenopteran parasitoids has ranged, up to 70% for ibaliid and rhyssine parasitoids collectively; parasitism by *I. leucospoides* is typically 20–40% in the wood-wasp's introduced range (reviewed in Hurley et al. 2007) and 22% in its native range (Spradbery and Kirk 1978). Parasitism by *D. siricidicola* has been more variable, ranging from 0 to nearly 100% in its southern hemisphere range (reviewed in Hurley et al. 2007), and is undescribed in the wasp's native range. For effective and consistent biological control, parasitism or infection of *S. noctilio* must be relatively consistent between locations and years, as well as throughout the bole of the tree. There is limited description of the within-tree variation in parasitism rates available. Penteado et al. (1998) show that within-tree distribution of *I. leucospoides* and of *D. siricidicola*-infected *S. noctilio* females follow the same general trend as the distribution of *S. noctilio*; however, their analysis was limited by a small number of *I. leucospoides* collected. Similarly, in the eastern United States of America, Eager et al. (2011) found that counts of both siricids and *I. leucospoides ensiger* were higher in *Pinus* spp. bolts that were between 14 and 20 cm in diameter, which could be expected to represent midregions of the bole.

Sirex noctilio emergence is highly variable in its native and introduced ranges, and varies from early or midsummer to early autumn (Ryan and Hurley 2012). The effect of nematode parasitism on *S. noctilio* emergence patterns is undescribed. The larval parasitoid *Rhyssa* spp. begin to emerge before *S. noctilio*, in spring or early summer and for 4–5 mo, whereas the egg parasitoid *I. leucospoides* has a flight season synchronized with *S. noctilio*'s (Chrystal 1928a, Morgan and Stewart 1966b, Neumann et al. 1987, Eager 2010).

The objectives of this study were: 1) to quantify the siricid parasitoid assemblage in *S. noctilio*-infested trees in south and central Ontario; 2) to estimate hypothetical percent parasitism by the known, common hymenopteran parasitoids of siricids, and the prevalence of nematode infection in *S. noctilio*; 3) to describe the spatial, and between-year, variability of parasitism by hymenopterans and nematodes; 4) to describe their within tree distribution; 5) to establish the seasonal pattern of parasitoid emergence in relation to that of siricids; and 6) to describe the emergence pattern of *S. noctilio* females with and without nematode infection.

Materials and Methods

The methodology of this study is identical to that described in Ryan et al. (2011). In brief, 60 *S. noctilio*-

infested *Pinus* spp. trees, as evidenced by the presence of resin beads on the bole (Ryan 2011), were collected from 17 forested sites (1–9 trees per site) in southern and central Ontario. For each tree, its diameter was measured at 1.3 m above the ground and its height was measured to the top of the crown. Trees were felled in May 2007 ($n = 22$ trees: 17 *Pinus sylvestris* L., five *Pinus banksiana* Lambert) and 2008 ($n = 38$ trees: 34 *P. sylvestris*, four *Pinus resinosa* Aiton). Trees were cut at the base (within 40 cm of the ground) and sectioned into 1-m-long bolts. Bolts were stood apex side up in individual emergence containers that were stored upright in covered, unheated, translucent-sided-sheds at Angus, Ontario (17T 589861 4908280). A full description of site and tree selection methods, tree collection location and attributes, and emergence container set up can be found in Ryan (2011). There is evidence that emergence of *S. noctilio* cohort can spread over two seasons in this region (Ryan et al. 2011), however, there were few parasitoid specimens emerging from the bolts in year 2 (12 *I. leucospoides* and no *Rhyssa* spp. from the 38 trees collected in 2008) so only specimens (siricids and parasitoids) emerging within six months of the felling date were included in this study.

All emerging insects were collected regularly (3–5 times per week) from each rearing container between May and October (inclusive); each collection was stored individually in a vial of 70% ethanol until insects could be processed in the laboratory. Siricids were identified using keys available in Schiff et al. (2006) along with supplementary material provided by H. Goulet (unpublished). Specimens keyed as *Sirex edwardsii* Brullé were combined with *Sirex nigricornis* F. for analyses because recent morphological studies and mitochondrial deoxyribonucleic acid data have revealed that both are discreet color morphs of a single species, *S. nigricornis* (H. Goulet, personal communication). Hymenopteran parasitoids of Siricidae were identified using Goulet and Huber (1993) and Nuttall (1980); subspecies of *I. leucospoides* was not determined because we found that the distinguishing characteristic (color) was too subjective.

The abdomen of each *S. noctilio* female was dissected to look for the presence of the nematode *D. siricidicola*. The presence of nematodes was recorded only when infection was unequivocal; in some cases this could not be determined because of insect desiccation or damage so these specimens were eliminated from the analysis of infection rates.

Data Analysis. Parasitism by hymenopteran parasitoids was calculated as a proportion of all *Sirex* spp. and parasitoid specimens emerging. Nematode infection rates were calculated as follows: infection rate = [no. of infected ♀♀ * 100/total number ♀♀]. Proportion data were arcsine square root transformed before the following analyses.

The influence of tree species and year of collection on parasitism rates by *I. leucospoides* and *D. siricidicola* were examined using trees from the 10- to 15-m height class (described below) to represent each tree species-year combination. There were four each of *P.*

Table 1. Mean \pm SE and total number of *Sirex* spp. specimens per tree (A) and mean \pm SE proportion of females and total females per tree (B) that emerged from 60 *Pinus* spp. trees with symptoms of *S. noctilio* attack cut down in 2007 ($n = 22$) and 2008 ($n = 38$) from 17 forests located in central and southern Ontario

	2007		2008		Total no. of specimens	Total no. of trees infested
	<i>P. banksiana</i> [5] ^a	<i>P. sylvestris</i> [17]	<i>P. resinosa</i> [4]	<i>P. sylvestris</i> [34]		
A Number of specimens						
<i>S. noctilio</i>	55.0 \pm 24.6 (5)	184.3 \pm 38.6 (17)	102.3 \pm 40.0 (4)	94.1 \pm 17.2 (34)	7018	60
<i>S. nigricornis</i>	0.6 \pm 0.6 (1) ^b	10.2 \pm 10.2 (2)	0	1.4 \pm 1.1 (6)	224	9
B Proportion of females						
<i>S. noctilio</i>	26.5 \pm 10.2% (5) ^c	23.8 \pm 3.2% (17)	65.6 \pm 6.2% (4)	25.1 \pm 2.8% (33)	1783	59
<i>S. nigricornis</i>	0	5.9 \pm 2.0 (1)	–	37.7 \pm 6.5 (4)	34	5

^a Number of trees felled is given in brackets [].

^b Number of trees infested with *Sirex* spp. is given in parentheses ().

^c Number of trees with females is given in parentheses ().

banksiana and *P. resinosa* meeting this criterion and several *P. sylvestris*, so four *P. sylvestris* per felling year were randomly selected to obtain samples of similar sizes. A Mann–Whitney *U* test was used for this comparison, as this data set could not be adequately transformed for parametric testing (Quinn and Keough 2002).

Data were examined for statistical correlation between *I. leucospoides* and *D. siricidicola* parasitism rates and tree characteristics (total height and diameter at breast height (dbh) in each year by using emergence data from *P. sylvestris* and Spearman’s rank correlation coefficient (Quinn and Keough 2002).

The influence of site and year on parasitism by *I. leucospoides* and *D. siricidicola* was evaluated in *P. sylvestris*. Only sites with a minimum of three *P. sylvestris* felled were selected for this investigation; when more than three trees had been felled in a site, three trees were selected at random. With this selection method, five sites per year were used in this analysis; two of these sites had trees collected from them in both collection years. Within each year (intersite variability), proportion parasitism per site was compared with a one-way analysis of variance (ANOVA). For the year-to-year comparison, parasitism rates from the two sites sampled in both years were evaluated with repeated measures ANOVA, and those from unique sites with ANOVA.

Intra-tree variation in parasitism rates was investigated by assigning trees to one of three arbitrary height classes (<10 m, 10–15 m, and >15 m). Each category was analyzed separately. Data could not be transformed to meet assumptions of parametric testing so within-tree (between bolt) parasitism rates of *I. leucospoides* and *D. siricidicola* in each tree species were analyzed with Friedman’s two-way ANOVA (Friedman 1939). In these models, parasitism rates were compared between the lower three (height class <10 m), four (10–15 m), or eight (>15 m) 1-m bolt sections, those common to each of the trees in the height category. All analyses were conducted in SYSTAT 12 (Systat Software Inc. 2007) with alpha set to <0.05.

Results

***Sirex* spp.** Two species of *Sirex* emerged during this study; 97% of the 7,242 specimens recovered were identified as *S. noctilio* and the remaining as *S. nigricornis* (Table 1a). *Sirex noctilio* specimens emerged from all 60 felled trees, whereas *S. nigricornis* emerged from nine trees. Of the 502 total bolts, 402 were colonized by woodwasps, and 385 of those were colonized only by *S. noctilio*. *Sirex noctilio* emerged from all three species of pines felled: *P. banksiana*, *P. resinosa* and *P. sylvestris*. *Sirex nigricornis* emerged only from *P. banksiana* and *P. sylvestris*. The mean density of *S. noctilio* per tree was lowest on *P. banksiana*. An average of \approx 25% of the specimens reared from these pine bolts were females: the only exception was on *P. resinosa* in 2008 when just over 65% of the specimens were females (Table 1b).

Parasitism and Infection. Nearly 2,500 specimens of hymenopteran parasitoids of Siricidae were obtained from 50 of the 60 *S. noctilio*-infested trees (Table 2a). *Ibalia leucospoides*, *R. lineolata*, and *R. p. persuasoria* emerged from 50, 18 and 11 trees, respectively. In total, 2,160 *I. leucospoides*, 154 *R. lineolata*, and 62 *R. p. persuasoria* emerged from bolts colonized exclusively by *S. noctilio*. A breakdown of the parasitoid assemblage per tree for each year revealed that more than one species can emerge from a single tree, but more often (>60%) a single species of parasitoid emerged. All three species of parasitoids were recovered from *P. banksiana* and *P. sylvestris*; however, *I. leucospoides* was the only species to emerge from *P. resinosa*. *Ibalia leucospoides* was the most abundant parasitoid emerging from all three tree species, and accounted for the highest proportion of parasitism when averaged over all 60 trees (Tables 2, 3). *Rhyssa p. persuasoria* emerged more commonly from *P. banksiana* and accounted for the highest proportion of parasitism in this tree species when per tree parasitism was averaged over the number of trees in which the parasitoid was present (Tables 2, 3). Overall, parasitism by these three species collectively was 23.4% (25.2% in 2007 and 22.4% in 2008); *I. leucospoides* accounted for 89% of that parasitism (Table 3). Parasitism of *Sirex* spp. by *I. leucospoides* did not vary between *P. banksiana* and *P. sylvestris* in 2007 ($U = 3.0, P = 0.15$), or between *P.*

Table 2. Mean \pm SE number of hymenopteran parasitoid specimens that emerged from 60 *Pinus* spp. trees with symptoms of *S. noctilio* attack cut down in 2007 ($n = 22$) and 2008 ($n = 38$) from 17 forests located in central and southern Ontario (A) and the breakdown of parasitoid diversity per tree (B)

	2007		2008		Total no. of specimens	Total no. of trees with parasitoids
	<i>P. banksiana</i> [5] ^a	<i>P. sylvestris</i> [17]	<i>P. resinosa</i> [4]	<i>P. sylvestris</i> [34]		
A: Number of specimens						
<i>Ibalia leucospoides</i>	48.4 \pm 42.0 (3) ^b	64.9 \pm 16.3 (15)	41.8 \pm 35.5 (3)	21.1 \pm 4.3 (29)	2,229	50
<i>Rhyssa lineolata</i>	3.4 \pm 2.7 (2)	2.3 \pm 0.9 (6)	0	3.0 \pm 1.2 (10)	158	18
<i>Rhyssa p. persuasoria</i>	9.4 \pm 8.7 (2)	0.2 \pm 0.1 (2)	0	1.6 \pm 1.2 (7)	105	11
B: Breakdown of parasitoid diversity per tree						
<i>I. leucospoides</i> only (A)	0	9	3	16	–	28
<i>R. lineolata</i> only (B)	0	1	0	0	–	2
<i>R. p. persuasoria</i> only (C)	0	0	0	0	–	1
A + B	1	4	0	6	–	11
A + C	1	1	0	3	–	4
A + B + C	1	1	0	4	–	4
Total no. trees with parasitoids	3	16	3	29	–	50

^a Number of trees felled is given in brackets [].

^b Number of trees with parasitoids is given in parentheses ().

resinosa and *P. sylvestris* in 2008 ($U = 6.5$, $P = 0.66$). Also, parasitism rates of *Sirex* spp. on *P. sylvestris* did not vary between years ($U = 10.0$, $P = 0.56$). There was a significant negative correlation between the proportion of *I. leucospoides* parasitism and *P. sylvestris* dbh in 2008 and a similar trend in 2007, but no relationship with tree height (Table 4).

Of the 1,783 *S. noctilio* females collected, qualitative assessment of the presence or absence of nematodes was performed on 1,445 specimens. When present, *D. siricidicola* were found in the haemocoel of the wood-wasp or in the egg sheath, rather than parasitizing the eggs. Of the females assessed for nematodes, 38% had nematodes in the haemocoel. Infection rates varied greatly among trees (0–100%). There was no difference in infection rates by *D. siricidicola* between *P. sylvestris* and *P. banksiana* in 2007 ($U = 2.1$, $P = 0.21$), however, rates observed on *P. resinosa* differed from those on *P. sylvestris* in 2008 ($U = 2.0$, $P = 0.05$), because no nematode-infected female emerged from *P. resinosa* (Fig. 1). Infection rates observed in *P. sylvestris* in 2007 did not differ from those in 2008 ($U =$

6.5, $P = 0.66$). There was a significant negative correlation between nematode infection and tree dbh in *P. sylvestris* in 2008 and a similar trend in 2007 (Table 4) but there was no significant relationship with tree height.

Variation in Parasitism and Infection Between Sites and Among Years. Parasitism rates by *I. leucospoides* did not differ between sites in 2007 ($F_{4,10} = 1.30$, $P = 0.33$) but did in 2008 ($F_{4,10} = 6.45$, $P = 0.01$). There was no significant difference in parasitism between years in the two sites sampled in both years ($F_{1,5} = 1.99$, $P = 0.22$) nor in the sites unique to each year ($F_{1,16} = 0.22$, $P = 0.65$).

Nematode infection rates differed significantly among the five sites sampled in 2007 ($F_{4,10} = 9.95$, $P = 0.002$), but not in 2008 ($F_{4,10} = 1.43$, $P = 0.29$). There was no difference in infection rates between years in resampled sites ($F_{1,5} = 1.88$, $P = 0.23$) or in the three unique sites ($F_{1,16} = 1.94$, $P = 0.18$).

Within-tree Distribution of Parasitism. The within-tree distribution of *S. noctilio* emergence for each category of *Pinus* tree height (Ryan et al. 2011) is

Table 3. Mean \pm SE percent parasitism of *Sirex* spp. that emerged from 60 *Pinus* spp. trees with symptoms of *S. noctilio* attack cut down in 2007 ($n = 22$) and 2008 ($n = 38$) from 17 forests located in central and southern Ontario

	2007		2008		Overall parasitism
	<i>P. banksiana</i> [5] ^a	<i>P. sylvestris</i> [17]	<i>P. resinosa</i> [4]	<i>P. sylvestris</i> [34]	
Percent parasitism per tree infested by <i>Sirex</i> spp. ($n = 60$)					
<i>Ibalia leucospoides</i>	17.9 \pm 10.7%	21.4 \pm 3.6%	15.2 \pm 9.0%	19.8 \pm 3.0%	19.80%
<i>Rhyssa lineolata</i>	1.6 \pm 1.0%	1.6 \pm 0.8%	0	2.8 \pm 1.1%	2.20%
<i>Rhyssa p. persuasoria</i>	13.1 \pm 12.2%	0.1 \pm 0.0%	0	0.6 \pm 0.4%	1.40%
Percent parasitism per tree in which the parasitoid is present					
<i>Ibalia leucospoides</i>	29.8 \pm 4.2% (3) ^b	24.3 \pm 3.5% (15)	20.3 \pm 10.6% (3)	23.3 \pm 3.2% (29)	
<i>Rhyssa lineolata</i>	4.0 \pm 0.2% (2)	4.6 \pm 1.8% (6)		9.6 \pm 1.7% (10)	
<i>Rhyssa p. persuasoria</i>	32.8 \pm 23.9% (2)	0.6 \pm 0.1% (2)		3.0 \pm 0.2% (7)	

^a Number of trees infested by *Sirex* spp. is given in brackets [].

^b Number of trees in which each parasitoid is present is given in parentheses ().

Table 4. Spearman's correlation coefficients for association between *S. noctilio* parasitism and *P. sylvestris* characteristics; trees collected from southern and central Ontario; $n = 17$ (2007), $n = 34$ (2008)

	Year	<i>Ibalia leucospoides</i>	<i>Deladenus sircidicola</i>
Tree ht	2007	0.33	0.19
	2008	-0.09	-0.29
Diameter at breast ht	2007	-0.23	-0.27
	2008	-0.35 ^a	-0.41 ^a

^a Significant at $P < 0.05$.

presented here to facilitate comparisons with that of parasitism by *I. leucospoides* and infection by *D. sircidicola* in the same categories (Fig. 2a-f). The proportion of *I. leucospoides* emerging from each bolt section was relatively uniform throughout the bole of *P. sylvestris* for the two smallest height classes, but not for trees >15 m felled in 2008; there was an absence of *I. leucospoides* parasitism in lower sections of the bole (Fig. 2a-f). In the other *Pinus* spp. within-tree parasitism rates did not differ and results are not presented.

Emergence Periods of Siricidae and Parasitoids. *Sirex noctilio* emerged between early-July and early-September in 2007 and 2008 (Fig. 3a, b) with the bulk of emergence occurring between mid-July and mid-August. *Sirex nigricornis* emergence began in early September of each year, and was largely concluded by the third week of September in 2007, and by the second week of September in 2008. The emergence period of *I. leucospoides* matched in time that of *S. noctilio*, whereas that of the *Rhyssa* spp. began in late May, about one month earlier than *S. noctilio* (Fig. 3a, b). Nematode-parasitized and un-parasitized *S. noctilio* emerged over a similar time period in both years, though the emergence of un-parasitized *S. noctilio* generally lagged behind that of parasitized in 2008 (Fig. 4a, b).

Discussion

Two species of Siricidae, *S. noctilio* and *S. nigricornis*, emerged from *Pinus* trees exhibiting symptoms of *S. noctilio* attack. *Sirex noctilio* emerged from *P. banksiana*, *P. resinosa* and *P. sylvestris* and was the most abundant woodwasp to emerge from these trees. In comparison, *S. nigricornis* emerged only from *P. banksiana* and *P. sylvestris* and accounted for ≈3% of *Sirex* spp. recovered in this study. The presence of *S. nigricornis* in *S. noctilio* infested trees was also reported by Long et al. (2009) who conducted a similar study in northeastern United States of America. The preponderance of *S. noctilio* over *S. nigricornis* in our sampled trees is unlikely to be the result either of competition between these species, or evidence of a rarity of *S. nigricornis*. The selection, and timing of felling, of these trees was designed to favor the collection of *S. noctilio*. Our results revealed the existence of a temporal difference in seasonal emergence and colonization patterns between these species, with *S. noctilio* emerging months before *S. nigricornis* (Fig. 3). Furthermore, the prevalence of *S. noctilio* compared with *S. nigricornis* could simply reflect a preference for hosts of a specific quality or condition. For example, *S. noctilio* favors living, albeit stressed or suppressed trees, whereas native woodwasp species colonize recently dead trees. Thus it could be hypothesized that *S. noctilio* has a direct, positive, effect on the availability of suitable hosts for *S. nigricornis*.

Females accounted for ≈25% of *S. noctilio* emerging from *P. sylvestris* and *P. banksiana*, and 65% from *P. resinosa*. The range in male:female sex ratio found in *P. sylvestris* and *P. banksiana* is similar to other areas of the wasp's introduced range (e.g., Zondag and Nuttall 1977, Iede et al. 1998, Hurley et al. 2008, Long et al. 2009). Male bias occurs as a result of facultative parthenogenesis; unfertilized eggs result in male offspring (Rawlings 1953). Mate finding is thought to be more difficult for *S. noctilio* when expanding into a new area or when populations are decreasing, thus resulting in higher male biased sex ratios (Morgan and Stewart 1966b; Ryan and Hurley 2012). However, this does not account for the higher proportion of females emerging from *P. resinosa*, which were extracted from the most northerly, and theoretically the more recently invaded, of the sites that we used.

Sirex noctilio was the sole woodwasp species to emerge from 51 of the 60 trees, and 385 of the 502 bolts. These numbers, though not proof, are consistent with the hypothesis that the hymenopteran parasitoids recovered from these bolts did parasitize *S. noctilio*. The hymenopteran parasitoid assemblage consisted of three known species of Siricidae parasitoid, *I. leucospoides*, *R. lineolata* and *R. p. persuasoria*. Of these three, *I. leucospoides* was the most abundant, accounting for 87% (2007) to 92% (2008) of the parasitoid specimens collected in each year and representing hypothetical parasitism rates of 16–23% of the *Sirex* spp. specimens. Overall *I. leucospoides* parasitism in this study was comparable to the 21.8% *I. leucospoides* parasitism reported for all woodwasps collectively in

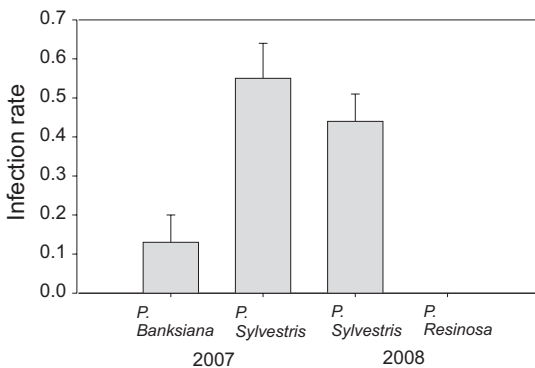


Fig. 1. Mean + SE proportion of female *S. noctilio* with nematodes in the haemocoel in *Pinus* spp. from southern and central Ontario in the first 6 mo after felling: *P. banksiana* ($n = 5$), *P. sylvestris* 2007 (17), *P. sylvestris* 2008 (34), and *P. resinosa* (4).

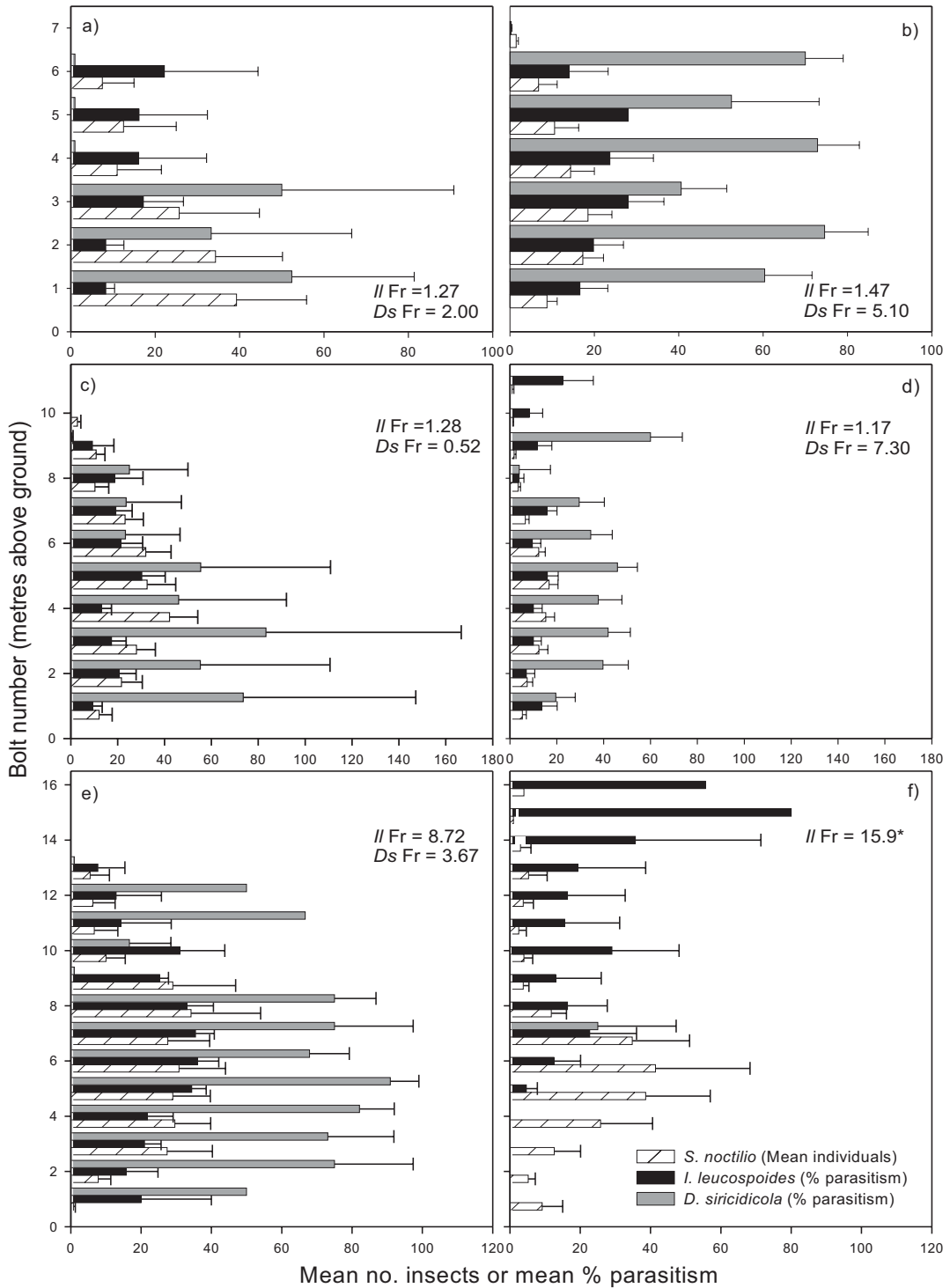


Fig. 2. Within-tree distribution of mean \pm SE number of emerging *S. noctilio* (data from Ryan et al. 2011), proportion of woodwasps parasitized by *I. leucospoides*, and proportion of *S. noctilio* females infected by *D. siricidicola* in three height categories of *P. sylvestris* collected over 2 yr from southern and central Ontario: a) <10 m 2007, $n = 3$ trees; b) <10 m 2008, $n = 11$ trees; c) 10–15 m 2007, $n = 9$ trees; d) 10–15 m 2008, $n = 18$ trees; e) >15 m 2007, $n = 5$ trees; f) >15 m 2008, $n = 5$ trees. Results of Friedman's one-way ANOVA (Fr) of intratree variation in parasitism by *I. leucospoides* (Il) and *D. siricidicola* (Ds) embedded (* significant at $P < 0.05$). Parasitism in lower three (<10 m), four (10–15 m) or eight (>15 m) 1-m sections compared. Note: Missing values represent data insufficient to analyze.

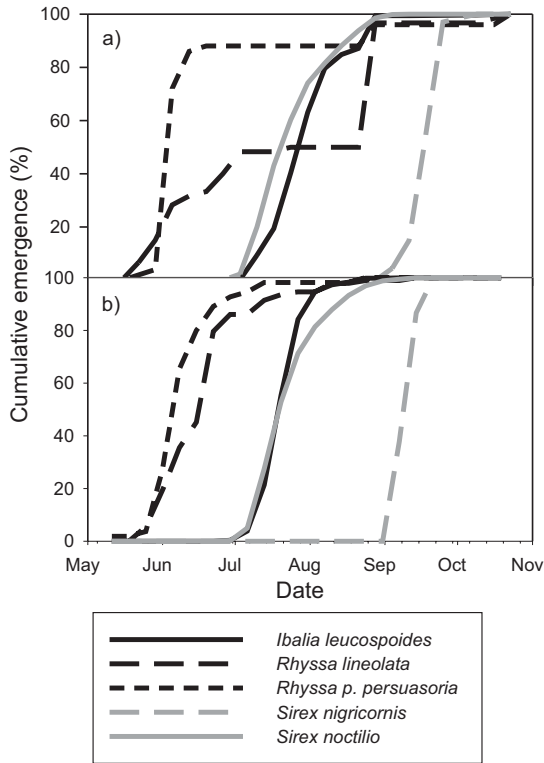


Fig. 3. Cumulative emergence over time of *Sirex* spp. and associated parasitoids collected live from *Pinus* spp. felled in southern and central Ontario a) 2007 ($n = 22$ trees, 1,336 *Ibalia leucospoides*, 58 *Rhyssa lineolata*, 73 *R. p. persuasoria*, 143 *S. nigricornis*, 2,286 *S. noctilio*); b) 2008 ($n = 38$, 882, 93, 55, 56, and 3,461, respectively).

S. noctilio's native European range (Spradbery and Kirk 1978), and similar to values reported for *S. noctilio* in many parts of its introduced range in the southern hemisphere (e.g., Neumann et al. 1987, Iede et al. 1998, Murphy 1998). The predominance of *I. leucospoides* in the parasitoid community is consistent with findings from other introduced regions, including adjacent areas of the United States of America (Collett and Elms 2009, Long et al. 2009). *Ibalia leucospoides* is believed to be a more efficient parasitoid, perhaps in part because it uses *S. noctilio* egg tunnels to locate its hosts. In contrast, *R. p. persuasoria* has poor host location abilities (Chrystal 1928a, Chrystal 1928b, Morgan and Stewart 1966b). However, as an egg parasitoid, *I. leucospoides* arrives first and may simply leave fewer resources for the *Rhyssa* species.

The proportion of parasitism by *I. leucospoides* was usually consistent within trees, and between sites and years. In most cases, there was no significant difference between percentage parasitism by *I. leucospoides* and bole height. Whether the lower levels of parasitism observed in the lower bole of *P. sylvestris* 15 m or more in height could be related to bark thickness is unknown (Penteado et al. 1998 but see Eager et al. 2011). Although there was some site-to-site variability in parasitism rates of *I. leucospoides* in *P. sylvestris* in

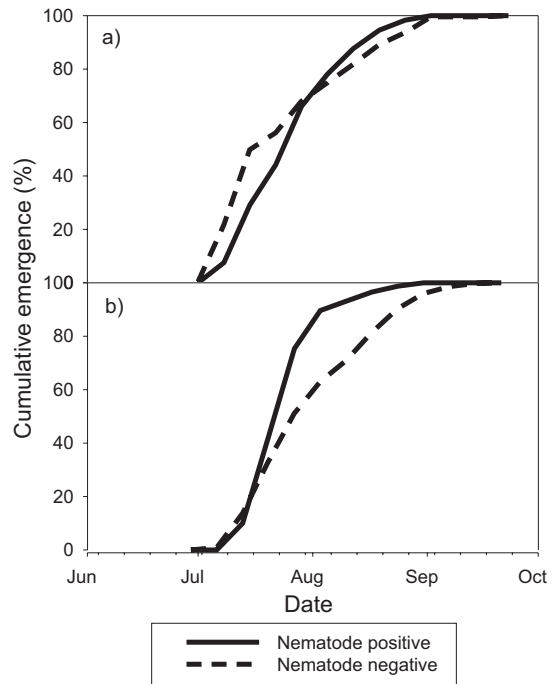


Fig. 4. Cumulative emergence of *D. siricidicola*-positive and -negative *S. noctilio* females in a) 2007 ($n = 22$ trees, 292 nematode-positive females, 203 nematode-negative females); b) 2008 ($n = 38$, 231, and 675, respectively).

one of the two study years, the lack of significant variation between sites in 2007, and between the 2 yr suggests relatively consistent levels of control by this parasitoid.

In our study, nematodes did not parasitize *S. noctilio* eggs, but rather were found exclusively in the haemocoel of females. This is similar to the findings of Yu et al. (2009) from *S. noctilio* specimens collected in a similar region of Ontario, Canada. This finding suggests that the eggs laid by these females are viable, and that this nematode strain does not sterilize the woodwasp in this region. Effective sterilization of females by the nematode is highly dependent on the strain of both the host and nematode (Bedding 1972). If the presence of the nematode affects the female woodwasp in other ways, such as by limiting its body size (and thus its fecundity) or affecting its dispersal ability, as seen in nematode-sterilized-females (Madden 1974, Villicide and Corley 2008), the nematode could function as a sublethal natural enemy. In much of the wasp's range in the southern hemisphere, *D. siricidicola* infection accounts for a higher rate of mortality than parasitoid wasps and it is thought to be the key factor controlling these woodwasp populations (e.g., Neumann and Minko 1981, Carnegie et al. 2005). However, nematode infection rates in the wasp's native range are undescribed and so is their relative role in controlling populations in native *Pinus* where *S. noctilio* is not an economic pest. Therefore, the significance of the lack of nematode sterilization in eastern

North America remains to be elucidated. The absence of *D. siricidicola* in *P. resinosa* could be an effect of differences in tree species; however, as these trees were collected from the most northerly sites in our study it may reflect climatic factors, or the delayed dispersal of the nematode relative to the woodwasp.

Both *S. noctilio* and *I. leucospoides* emerged over a similar time period in July and August while *Rhyssa* spp. emerged earlier, in late spring. This pattern of emergence is similar to that described elsewhere (Chrystal 1928a, Morgan and Stewart 1966b, Taylor 1978, Eager 2010). The pattern of parasitoid species emergence corresponds well to their life histories: *Rhyssa* spp. parasitize late instars in early summer, before woodwasp emergence, whereas *I. leucospoides* is an egg and early instar parasitoid and must emerge later (Taylor 1978). This description of the emergence pattern of *Sirex* spp. and their parasitoids in the woodwasp's North American range is the first description of the timing of emergence of these species.

Our study from several sites in southern Ontario provides a comprehensive assessment of the composition, structure, within-tree distribution and hypothetical impact of the hymenopteran parasitoid assemblage of *S. noctilio* in eastern North America. It also provides a first glance at the ubiquity of, and unique role played by, the parasitic nematode *D. siricidicola* in the dynamics of this woodwasp. This study affirms the importance of *I. leucospoides* as a primary parasitoid of Siricidae in general and of *S. noctilio* in particular. Our study also provides some insight into the apparent constancy in parasitism of *S. noctilio* in space (among sites) and time (between years) and highlights the lack of consistent influence of tree species, height, and dbh. Finally, this study provides key information on the seasonal pattern of woodwasp emergence and that of its parasitoids.

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