

RESEARCH ARTICLE

Suitability of eastern pines for oviposition and survival of *Sirex noctilio* F.

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Abstract

The European woodwasp, *Sirex noctilio* F., is a pest of pines in many areas around the world. Since its introduction to North America, the distribution of *S. noctilio* overlaps with a known host (*Pinus sylvestris*) and hosts native to North America. Direct comparisons of suitability for oviposition and larval survival among these pines have not been made. We tested the relative suitability of four common pine species in northeastern North America (*P. sylvestris*, *P. resinosa*, *P. banksiana*, and *P. strobus*) as hosts for *S. noctilio* in a controlled, but *in situ* experiment. In a mixed pine forest in northern Ontario, we caged *S. noctilio* mating pairs on 10 freshly cut pine logs of each species, and estimated oviposition, counted adult *S. noctilio* (F1 generation) that emerged from logs, and calculated survivorship from egg to adult. *Pinus sylvestris* and *P. resinosa* were optimal hosts according to all three metrics of *S. noctilio* performance. *Pinus strobus* was a suitable larval host, but was not perceived as such by females, as evidenced by lower oviposition. *Pinus banksiana* was perceived as a suitable host by females, but was the least suitable larval host. Our results suggest that *P. sylvestris* and *P. resinosa* are more suitable hosts, at least in cut logs, than *P. strobus* and *P. banksiana* for *S. noctilio* in eastern North America.

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Introduction

The European woodwasp, *Sirex noctilio* F., is a wood-boring pest of pines (*Pinus*) in many, but not all, parts of the world where it has been introduced [1]. *Sirex noctilio* is especially aggressive in areas of the Southern Hemisphere where natural enemies and other wood-boring competitors are absent and exotic pines are planted in monocultures that are not well-managed [1, 2]. Though it has not been a destructive pest in North America since its discovery in 2004 [3, 4], *S. noctilio* has potential to impact pine forests of varying species compositions differently as it spreads. In North America, the range of *S. noctilio* overlaps with *P. sylvestris* (Scots pine), *P. resinosa* (red pine), *P. banksiana* (jack pine), and *P. strobus* (eastern white pine) [5–7]. *Sirex noctilio* shares a co-evolutionary history with *P. sylvestris* (both are native to Europe), which is widely planted and considered naturalized in eastern North America [8]. The other three pines are native to North America and do not share a co-evolutionary history with *S. noctilio*. Understanding the relative suitability of these pines for *S. noctilio* oviposition and larval

development is critical for predicting whether and where the woodwasp could become an aggressive pest in North America as it spreads.

Offspring (brood) success in endophytic insects is determined by a combination of perceived suitability of the larval host by the female and actual suitability of the host habitat for larval development [9–11]. Volatiles (α - and β -pinene, carene, and others) emitted by stressed pines attract female *S. noctilio* [12–14]. The female first assesses the bark with her antennae, then probes and eventually drills into the bark with her ovipositor [15]. She determines the suitability of the tree for larval development based on osmotic (resin) pressure in the phloem, and will not oviposit in trees with high osmotic pressure [16–18]. If osmotic pressure is high, she may still inject a fungal symbiont, usually *Amylostereum areolatum*, and a phytotoxic venom that function in combination to weaken the tree's vascular system [16–20]. If osmotic pressure is low, the female considers the tree a suitable host, and she will also inject one or more eggs in or near her initial drill site [16–18].

Less is known about what constitutes a suitable larval host. Tree resistance likely plays a primary role in dictating whether small larvae survive, and was the most important mortality factor during *S. noctilio* development according to life tables [21]. Pines resist *S. noctilio* constitutively by flooding oviposition drills with resin [22], and by induced accumulation of polyphenols in the sapwood surrounding the oviposition site [22, 23]. Both of those mechanisms are likely compromised in stressed trees. It is not known how host tree condition relates to nutritional quality for developing larvae, partly because the source(s) of larval nutrition is(are) unclear. Larvae chew wood, but pass it underneath the body instead of through the digestive tract, and may feed on liquid extract digested first by the fungus to release starch and sugars [24]. Bacteria may also provide nutrition for *S. noctilio* larvae, either through cellulose digestion, provision of sterols, and/or nitrogen fixation [24–26].

Despite unknowns surrounding host suitability for *S. noctilio* larvae, there are many host reports from around the world. *Sirex noctilio* attacks and develops in many different pines, and while some species seem to be preferred hosts, or at least more suitable hosts than others, no pines appear to be resistant [27]. This suggests that *S. noctilio* and its fungal symbiont are well-adapted to develop in all species of the Pinaceae. Fir (*Abies*) and spruce (*Picea*) are occasional hosts for *S. noctilio* in its native range, though far less frequently than pines [15, 28]. In Europe, *S. noctilio* colonizes the native pines, *P. pinaster* and *P. sylvestris* more frequently than *P. radiata* (not native to Europe) [28–30]. In the Southern Hemisphere, *S. noctilio* commonly colonizes *P. radiata*, *P. taeda*, *P. elliotti*, *P. ponderosa*, and *P. patula* [1, 31–33].

In North America, observational studies reported that *P. sylvestris* is likely a more favorable and/or suitable host than other pines. *Sirex noctilio* attacks and kills more trees in *P. sylvestris* than in *P. resinosa* forests [5, 29]. In naturally infested trees collected from different sites, larger broods of *S. noctilio* and its parasitoids were observed in *P. sylvestris* than in *P. resinosa*, *P. banksiana*, or *P. strobus* [6, 7, 34, 35], although none of those studies compared all four pine species at once. In a study where co-occurring *P. sylvestris* and *P. resinosa* were artificially stressed with herbicides, *S. noctilio* brood from *P. sylvestris* were 25% larger in densities three times greater than brood from *P. resinosa* [36]. Direct comparisons of the suitability of different pines in controlled settings have not been made.

Our objective was to test the relative suitability of four common pine species in northeastern North America (*P. sylvestris*, *P. resinosa*, *P. banksiana*, and *P. strobus*) as hosts for *S. noctilio* in a controlled, but *in situ* experiment. We tested whether pine species affected *S. noctilio* (1) oviposition, (2) F1 brood production, and (3) survivorship, as well as (4) abundance of parasitoids. Based on observations from previous studies, we predicted that *S. noctilio* oviposition, F1 brood production, and survivorship would all be greater in *P. sylvestris* than in the other pines.

Materials and methods

Study site and adult *S. noctilio* collection

The study site was a mixed pine-hardwood (maple, birch) forest (UTM Zone 16T, 692978 E, 5152387 N) near Sault Ste. Marie, Ontario, Canada, where pole-sized pines of each species grew. No specific permission was required to use this study site, as the land was owned by the Canadian Forest Service. We found evidence of *Sirex* at the study site, via resin beading [37] on the trunks of a few dying *P. sylvestris*. This resin beading could have been from *S. noctilio*, or the closely related native species, *S. nigricornis*. Although *S. noctilio* was not confirmed as present in the area at the time this study began (July 2014), *S. nigricornis* was and because it has the same parasitoid complex as *S. noctilio* in eastern North America [38], we expected that the parasitoids, *Ibalia leucospoides* (Hymenoptera: Ibalidae) and *Rhyssa persuasoria* and *R. lineolata* (Hymenoptera: Ichneumonidae), would be present at the study site, as well as competing wood borers, *Monochamus* spp. (Coleoptera: Cerambycidae).

We introduced adult *S. noctilio* to freshly cut pine logs, enclosed in cages at our study site (see *Experimental set-up* below). These adult *S. noctilio* were obtained from naturally infested pines (identified by resin beading), which we felled and removed from several sites throughout southern Ontario (see [39] for details on locations). In late June of 2014, we brought infested pine logs to a field station near Barrie, Ontario, where we placed them into cardboard rearing tubes in a covered, outdoor shed. We collected *S. noctilio* that emerged from the logs 5x per week and stored them at 4°C until enough were available for a shipment (20+ wasps). We shipped the wasps to Sault Ste. Marie overnight in coolers with ice packs (1–2 times per week).

Experimental set-up

We selected 10 pole-sized pines (diameter at breast height: 6–8 cm) of each species. We felled five trees of each species during the first week of July, and five more during the second week of July (to prepare for staggered availability of adult *S. noctilio*). As described in Haavik et al. [21], we cut a 3–4 m section from the mid-bole of each tree and placed each end of these logs onto a cinder block (25x10x10 cm). On the same day, we then secured two wire mesh (2x2 mm) screen cages (1 m long) to each horizontal log with heavy duty, plastic zip-ties at each end. The cages were equipped with Velcro® closures, sewn directly onto the wire mesh. To prevent cages from collapsing in on themselves, we screwed three wooden struts (10–15 cm long, cut from 5x5 cm lumber) into logs, equidistant apart (e.g., at 0°, 120°, and 240°), near both ends of cages, and encircled the struts in a hoop of plastic tubing (1.75 cm in diameter), screwed to the struts. The logs were arranged in a randomized complete block design in a clearing within the mixed pine-hardwood forest.

In an attempt to create a physically suitable (i.e., stressed) host tree for optimal survival of the *S. noctilio* F1 generation (see [40]), we felled and caged trees 1.5–3 weeks before introducing *S. noctilio* mating pairs to cages. Each cage received two male-female pairs of *S. noctilio* (i.e., 4 wasps per cage, 8 wasps per tree, 80 wasps per treatment, 320 wasps total [160 males, 160 females]). To expose one-half of each log to associates (competitors + parasitoids) (n = 10 logs per pine species), we removed one cage from each log (top or bottom section decided at random by a coin flip) 1–2 weeks after wasps were inserted into cages. At this time all females were dead, and had presumably oviposited on logs. The remaining bole sections were protected from associates, and cages were left on logs (n = 10 logs per pine species) throughout development of the F1 generation to protect them from associates.

In late June of 2015, just prior to expected completion of the F1 generation, we removed logs from the field site, and returned them to rearing drums in the lab. We collected emerging

adult wasps 2–5 times per week through October 2015. After adult emergence was complete, we peeled the bark from logs with a drawknife to reveal the sapwood surface. To estimate the number of eggs oviposited by female *S. noctilio* into the wood, we used a dissecting microscope (6.4x), positioned over the log surface, to count the number and type (single, double, triple, etc.) of oviposition drills (see [16] for details on this method).

Data analysis

We used an equation developed by Madden [16], which we tested and used previously [21], to estimate the number of eggs oviposited by female *S. noctilio* (i.e., realized fecundity) based on oviposition drill type (Total no. eggs = $0.04 \times \text{no. single drills} + 0.68 \times \text{no. double drills} + 1.55 \times \text{no. triple drills} + 2.22 \times \text{no. quadruple drills}$).

In the R statistical environment [41], we examined histograms of response variables to determine appropriate models and error terms. All were nested models with tree as a random factor and cage (exposed or protected from associates) and pine species as fixed factors. Interaction terms were not significant, so we removed them from models. The effects of cage and pine species on number of eggs was tested with a generalized linear model with a negative binomial distribution of errors (package = MASS), and differences among species were investigated with least squares means. We used a hurdle model with a negative binomial distribution of errors (package = pscl) to test for the effects of cage and pine species on number of *S. noctilio* adults. Relative to generalized linear models, hurdle models are advantageous because zero and non-zero responses are tested separately [42]. Hurdle models determine if the frequency of zero responses differs more than by chance among the treatments [42]. The effects of cage and pine species on survivorship from egg to adult (only trees in which eggs were oviposited were tested) was tested with a generalized linear model with a binomial distribution of errors (package = stats), and differences among species were investigated with least squares means. Too few parasitoids and competitors were collected from logs for statistical analysis. Statistical significance was set at $\alpha = 0.05$.

Results

Sirex noctilio oviposition occurred in 62 of the 80 logs in the entire study. We estimated that a total of 2,661 eggs were oviposited in the logs by *S. noctilio*; 732 in *P. banksiana*; 710 in *P. resinosa*; 1,110 in *P. sylvestris*; and 110 in *P. strobus*. In total, 145 *S. noctilio* adults (F1 generation) were recovered from the logs (overall survivorship from egg to adult = 5%); 6 from *P. banksiana*; 53 from *P. resinosa*; 64 from *P. sylvestris*; and 22 from *P. strobus*.

Significantly fewer *S. noctilio* eggs were oviposited in *P. strobus* compared with the other species ($z = 4.16$; $df = 3,76$; $P < 0.001$), which did not differ significantly from one another (Fig 1). Among logs that produced *S. noctilio* brood adults (29 of 80), the number of *S. noctilio* produced by *P. sylvestris* and *P. resinosa* were greater than the number produced by *P. banksiana* ($z = 2.55$; $df = 9,19$; $P = 0.012$), and the number produced by *P. strobus* did not differ significantly from the other pine species (Fig 2). The number of logs that did not produce adult *S. noctilio* (51 of 80) was greater for *P. banksiana* (16) than for *P. sylvestris* (9) ($z = 2.21$; $df = 9,41$; $P = 0.027$); *P. resinosa* (12) and *P. strobus* (14) did not differ significantly from the others. Survival from egg to adult was greatest in *P. strobus* ($z = 4.10$; $df = 3,58$; $P < 0.001$), intermediate in *P. sylvestris* and *P. resinosa* ($z = 4.65$ and 5.25 , respectively; $df = 3,58$; $P < 0.001$), and lowest in *P. banksiana* ($z = 4.10$; $df = 3,58$; $P < 0.001$) (Fig 3).

The effect of exclusion cage on estimated number of *S. noctilio* eggs, number of brood adults, or survivorship was not significant in any of the models ($P > 0.05$ for all). No *Rhyssa* individuals were recovered from the exposed logs. Few *Ibalia leucospoides* emerged from any

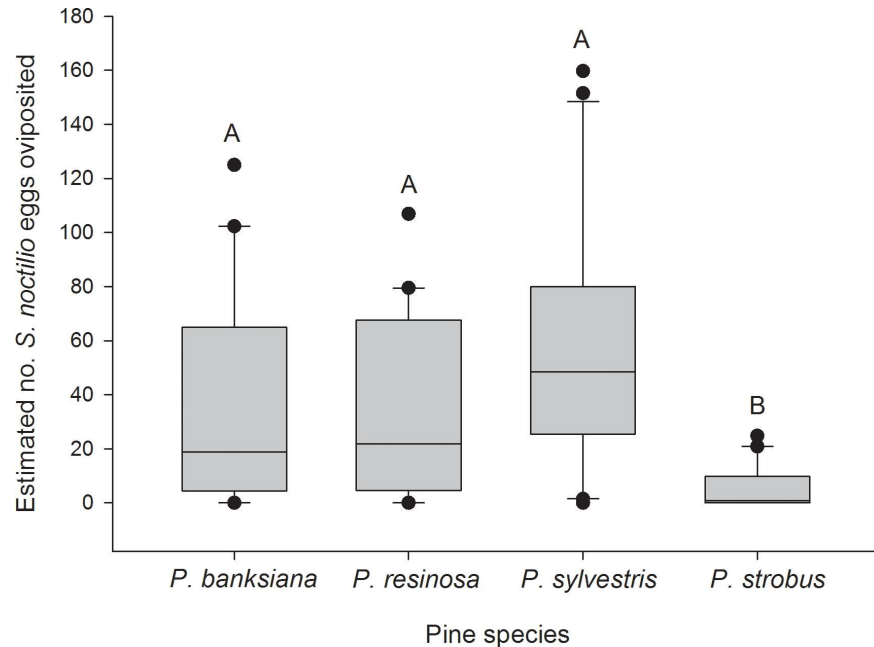


Fig 1. Boxplots of estimated number of eggs oviposited by *Sirex noctilio* in each pine species. n = 20 logs per *Pinus* species. Boxes are bounded by the first and third quartiles; the internal solid line represents the median.

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of the exposed logs (14 in total). No *I. leucospoides* emerged from *P. banksiana*; one emerged from a *P. strobus* log; one, two, and three emerged from three different *P. resinosa* logs; one, three, and three emerged from three different *P. sylvestris* logs. No Cerambycidae individuals

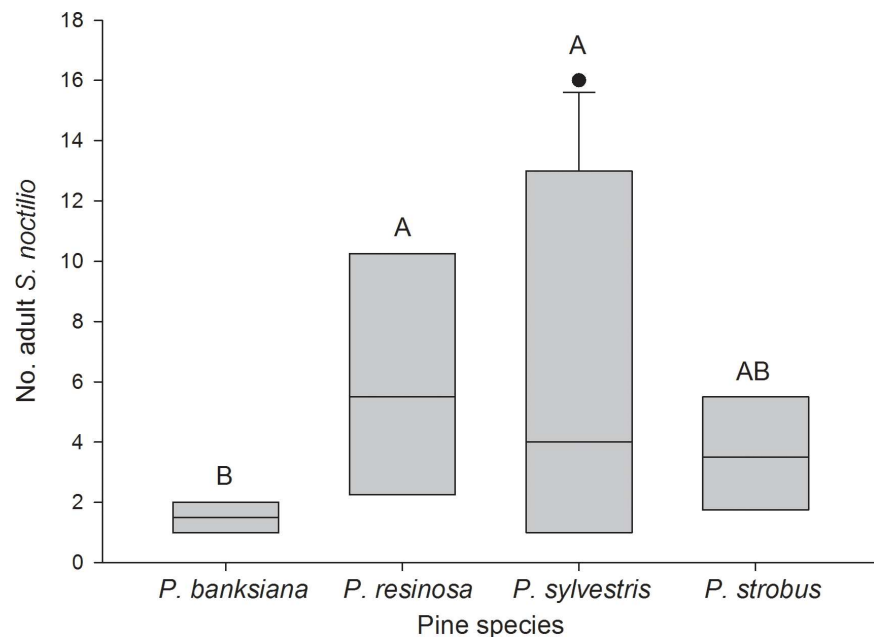


Fig 2. Boxplots of number of adult *Sirex noctilio* that emerged from each pine species. n = 4 logs for *Pinus banksiana*; n = 8 logs for *P. resinosa*; n = 11 logs for *P. sylvestris*; n = 6 logs for *P. strobus*. Logs that did not produce *S. noctilio* adults were excluded. Boxes are bounded by the first and third quartiles; the internal solid line represents the median.

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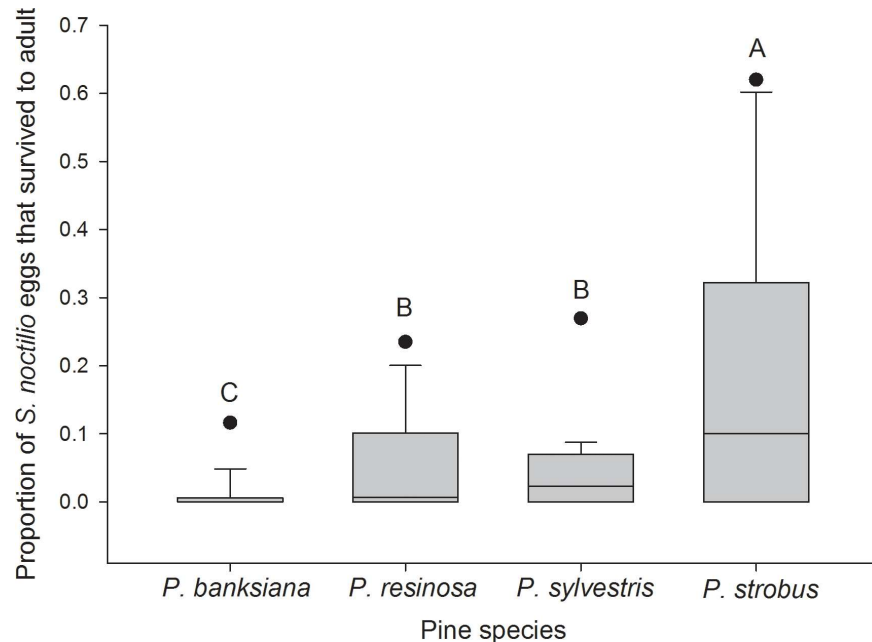


Fig 3. Boxplots of the proportion of *Sirex noctilio* eggs that survived to adulthood in each pine species. $n = 16$ logs for *Pinus banksiana* and *P. resinosa*; $n = 19$ logs for *P. sylvestris*; $n = 10$ logs for *P. strobus*. Boxes are bounded by the first and third quartiles; the internal solid line represents the median.

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were recovered from the logs. A few bark beetles (Scolytinae) were recovered from the exposed logs, but were not counted. We expected that at least some associates had already exited logs by late June of 2015 (when logs were removed from the field site).

Discussion

Pinus sylvestris and *P. resinosa* were equally suitable hosts for *S. noctilio*, both in perception by females and in brood production and survivorship from egg to adult. *Pinus strobus* was a suitable larval host, but was not perceived as such by females. *Pinus banksiana* was perceived as a suitable host by females, but was the least suitable larval host of all pine species (smallest brood, lowest survivorship, and most logs with no brood). Survivorship from egg to adult was very low among all pine species (5%), much lower than that reported by Taylor [43] in *P. radiata* (36–71%). Those studies measured survival in naturally attacked pines, which female *S. noctilio* selected as suitable larval hosts, whereas our study forced that interaction by not providing females with a choice of hosts of varying condition. In our previous study that used the same method, survivorship was also low (1–14%) [21]. It is likely that in felling trees 1.5–3 weeks before *S. noctilio* oviposition we created controlled experimental conditions, but failed to artificially create optimal hosts for larval development.

Our results relate to the preference-performance hypothesis (PPH, also called the mother-knows-best hypothesis) [9, 10]. The PPH predicts that females will choose to lay eggs on the host plant that is optimal for larval survival and development [9, 10]. Though *S. noctilio* females were not presented with a choice of larval hosts in our study, which precluded a direct test of the PPH, their behavior was consistent with the PPH only some of the time. Females apparently chose not to oviposit at all in some cases, especially on *P. strobus*, which turned out to be a good host for larvae. In contrast, *S. noctilio* females were apparently not able to detect that *P. banksiana* would not be an optimal larval host.

With a few exceptions [11, 44], the PPH theory was supported in a majority of empirical studies, compared via meta-analysis [44]. Specifically, Gripenberg et al. [44] found that in many insects, females laid more eggs on plants that were the most suitable for offspring, and more offspring survived on these preferred hosts. The PPH was especially well supported among insects that were oligophagous, having an intermediate host range, compared with insects that were polyphagous or monophagous [44]. The PPH was supported among oligophagous insects that, like *S. noctilio*, live and feed as larvae in woody tissues, such as the emerald ash borer (*Agrilus planipennis*) [45], the eucalyptus longhorned borer (*Phorocantha semipunctata*) [46], and the brown spruce longhorn beetle (*Tetropium fuscum*, stressed vs. healthy hosts of same species) [47]. In a polyphagous wood-boring insect, the Asian longhorned beetle (*Anoplophora glabripennis*), females only sometimes chose the host that also conferred optimal larval survival [48]. Although *S. noctilio* is oligophagous, based on our results, we predict that females would not consistently choose optimal hosts for larval survival and development, if given a choice.

Perhaps host acceptance cues varied among the different pine species. Böröczky et al. [14] found that a *P. sylvestris* chemotype with high amounts of the volatile carene was more attractive to female *S. noctilio* than *P. strobus* and a *P. sylvestris* chemotype with less carene, which suggests that host volatiles could be important in oviposition decisions. This highlights the need for a better understanding of the complete chemical volatile profiles of eastern pines and their relative attractiveness to *S. noctilio* females. Blends of α/β -pinene [49] or ethanol + α -pinene [50] were especially attractive to Siricidae native to North America. Bark texture may also be an important host cue. Other wood-boring insects that lay eggs on bark often prefer rough, or cracked bark over smooth bark [51, 52], presumably because bark fissures provide protection from natural enemies and environmental extremes, or provide a tight spot in which newly hatched larvae can attain leverage to chew and burrow into the bark. *Sirex noctilio* females have a different oviposition strategy, and drill past the bark to lay eggs directly in the sapwood. Still, smooth bark, such as that on *P. strobus*, may interfere with the female's purchase during drilling; or, perhaps more likely, smooth bark may be more accessible to parasitoids, especially those with short ovipositors, like *I. leucospoides*.

There are very few empirical examples that support the idea that female herbivorous insects seek enemy-free space for oviposition [10, 53]. Female *S. noctilio* avoidance of smooth-barked *P. strobus* may be an adaptation to avoid parasitoids. Unfortunately, the environment in our study site did not appear to support a very sizable parasitoid population to test this, as evidenced by the fact that *S. noctilio* survival was not affected by protection from natural enemies. Further, *I. leucospoides* attraction to and oviposition on different pine species may be an indirect response influenced by density of *S. noctilio* larvae present in a tree rather than the species of tree. Studies show that *I. leucospoides* is an efficient forager that can discern abundance of *S. noctilio* larvae in pine logs from a distance [54, 55].

Conclusions

Among the four potential host species evaluated, *P. sylvestris* and *P. resinosa* were optimal hosts for *S. noctilio* larval survivorship. We found little difference between *P. sylvestris* and *P. resinosa* as hosts for *S. noctilio*. This conflicts with observational studies that suggested *P. sylvestris* is a better host for *S. noctilio* than *P. resinosa*, *P. banksiana*, and *P. strobus*. There may be differences in attraction and suitability of living trees (those studies) versus cut logs (our study). In addition, those studies compared the relative number of *S. noctilio* brood adults produced by the different pine species that were colonized by ambient populations of *S. noctilio* [6, 7, 34, 36], or the relative number of different pine species that were killed by *S. noctilio* in

different stands [5, 29]. In those studies, it is likely that the local population density of *S. noctilio*, host condition, and availability of suitable hosts all played a larger role than actual differences in suitability of the two pine species as hosts for *S. noctilio* larvae. For example, in eastern North America, *P. resinosa* forests are more economically important and more heavily managed than *P. sylvestris* forests, and would be less likely to have as many hosts in a stressed condition suitable for *S. noctilio* survival and population growth.

Supporting information

S1 Table. Data collected from each log sample. Data includes number of *Sirex noctilio* eggs oviposited by females in the parent generation (estimate; see text for details), and number of adult *S. noctilio* in the F2 generation. (DOCX)

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Formal analysis: LJH.

Funding acquisition: LJH KJD JDA.

Investigation: LJH JDA.

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Project administration: LJH JDA.

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Software: LJH.

Supervision: LJH JDA.

Validation: LJH JDA.

Visualization: LJH.

Writing – original draft: LJH.

Writing – review & editing: LJH KJD JDA.

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