

Effect of *Sirex noctilio* (Hymenoptera: Siricidae) attack density on *Pinus sylvestris* (Pinaceae) survival

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Abstract—Population density is often a critical factor in colonisation of trees by bark and wood-boring insects and may determine whether an exotic species is likely to establish and spread. In a manipulative field study, we investigated whether density of the attacking population of an exotic invasive woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), affected survival and time-to-death of a favoured host tree, *Pinus sylvestris* Linnaeus (Pinaceae). We introduced mating pairs of woodwasps to stressed *P. sylvestris* at either high (15 mating pairs, nine trees) or low (two mating pairs, nine trees) density. More trees died, and more quickly, when exposed to the high versus low density of *S. noctilio* (78% versus 33% of trees). In the high-density treatment, year of tree death was synonymous with production of a *S. noctilio* F1 cohort (one-year or two-year generation time); this pattern was not as consistent in the low-density treatment. Although sample size was limited, our results indicate that attack density affects *S. noctilio* colonisation of *P. sylvestris*.

Population density is often a critical factor in colonisation of trees by bark and wood-boring insects. Insect population density can affect success in attack of individual trees (e.g., via compromised tree resistance), rate of tree mortality, stand-level mortality, and survivorship and fecundity in the subsequent generation. There is evidence that at high densities wood borers are able to mitigate or overcome host tree resistance more easily or quickly (Hanks *et al.* 1999; MacQuarrie and Scharbach 2015). Similarly, other studies observed that tree mortality was greater at sites with higher populations of wood borers (Fierke *et al.* 2007; Nahrung *et al.* 2014). Bark beetles (Coleoptera: Curculionidae) rely on high population densities to successfully kill and colonise host trees (e.g., Raffa and Berryman 1983), although at very high densities a trade-off between host colonisation and intraspecific competition exists (Lindgren and Raffa 2013).

It follows that density-dependent changes in offspring survival and parent generation fitness can also occur (Anderbrant *et al.* 1985; Jactel and Lieutier 1987; Zhang *et al.* 1992).

Sirex noctilio Fabricius (Hymenoptera: Siricidae), the European woodwasp, typically colonises stressed or sub-dominant pines (*Pinus* Linnaeus; Pinaceae) throughout its native range and in parts of its introduced range (Madden 1988; Ayres *et al.* 2014). However, *S. noctilio* is known to attack and, in some instances, successfully colonises greater numbers of healthy, co-dominant trees at high population densities or during an outbreak (Morgan and Stewart 1966; Madden 1975; Haavik *et al.* 2016). In North America where *S. noctilio* is exotic, it colonises native pines and a co-evolved pine, *Pinus sylvestris*, especially suppressed individuals (Dodds *et al.* 2010; Haavik *et al.* 2016). Although established and spreading in North America, *S. noctilio* has

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yet to outbreak and kill healthy pines at economically important levels (Ayres *et al.* 2014; Haavik *et al.* 2018), as it has done on other continents that it has invaded (Hurley *et al.* 2007).

Female *S. noctilio* inject the combination of a toxic mucus and symbiotic Fungi, *Amylostereum* Boidin (Amylostereaceae), into the tree (during or instead of oviposition) that weakens pine resistance to colonising larvae (F1 cohort) (Morgan and Stewart 1966; Coutts and Dolezal 1969). Typically, trees that are successfully colonised die, although several successive years of attack may be necessary to kill trees (Haavik *et al.* 2018). The effect of density of the attacking *S. noctilio* population on occurrence and time to tree mortality has not been empirically tested.

Our objective was to determine whether density of the attacking population of *S. noctilio* affected *P. sylvestris* survival. Specifically, we caged high and low densities of *S. noctilio* on *P. sylvestris* trees and examined whether *S. noctilio* attack occurred by the presence of characteristic resin beading, and whether attack was successful, as indicated by emergence of a F1 cohort. Subsequent to attack, we assessed if and when *P. sylvestris* mortality occurred. We expected that a higher population density of attacking *S. noctilio* would result in certain rapid mortality of *P. sylvestris*.

The study site was a *P. sylvestris* stand (UTM Zone 16T, 692978 E, 5152387 N) near Sault Ste. Marie, Ontario, Canada. Trees were pole-sized (diameter at a breast height of 6–8 cm) and experiencing sub-optimal growing conditions, as evidenced by crown dieback, and exhibited no evidence of infestation by the native *S. nigricornis*. The study site was not within the area generally believed to be infested with *S. noctilio* in 2014. We selected 18 *P. sylvestris* for our study that were haphazardly scattered throughout the stand and stressed by environmental factors enough that they exhibited $\geq 75\%$ crown dieback. We expected that these individuals would be suitable for *S. noctilio* colonisation.

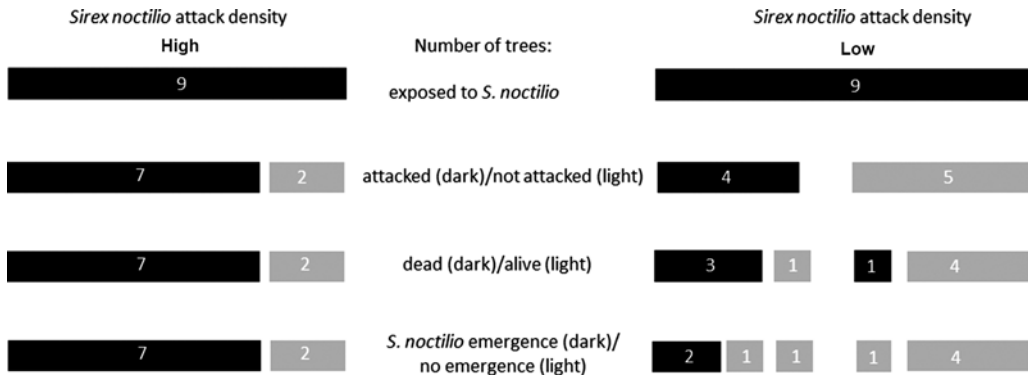
We tested two levels of *S. noctilio* population density: high (15 mating pairs) versus low (two mating pairs). In early July 2014, we used an orchard ladder to fit each tree with one (low-density treatment) or three (high-density treatment) wire mesh screen (2 × 2 mm) cages near mid-bole. We secured cages (each 1 m long) to tree boles 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 5 × 5 cm lumber) into tree boles, equidistant apart (*e.g.*, at 0°, 120°, and 240°), near both ends of cages.

In late July through mid-August 2014, we introduced male–female *S. noctilio* pairs to cages as wasps became available, partially completing one replicate from each treatment group at a time. This simulated natural conditions by creating some asynchrony in attack consistent with four to six week flight phenology (Ryan *et al.* 2012). The first wave of attacking females could condition (weaken) trees before more were introduced to complete the requisite number of wasps for the treatment. These adult *S. noctilio* were obtained from 58 naturally infested pines (identified by resin beading), which we felled and removed from several sites throughout southern Ontario. In late June of 2014, we brought those 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 five times 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 (one to two times per week). The number of replicates for this study was limited by availability of female *S. noctilio*, which were difficult to recover from a natural population that was low, because infested trees were difficult to locate, and sex ratios were often biased in favour of males (see Haavik *et al.* 2016, Table S1).

In September 2014, we determined whether trees were attacked by female *S. noctilio* by visual assessment of resin beading on tree boles inside the cages. Adult *S. noctilio* were not removed from the cages, and cages remained on trees throughout the duration of the study to prevent other insects from interfering with developing F1 *S. noctilio*. Only one tree (high-density treatment) was attacked by bark beetles during the study; it was also successfully colonised by *S. noctilio*. We assessed status of trees (alive versus dead) monthly from September 2014 to August 2015. In November 2015, we assessed and marked presence/absence of *S. noctilio* adult emergence holes

Fig. 1. Diagram illustrating the status and fate of 18 *Pinus sylvestris* two years following exposure to two different densities of attacking *Sirex noctilio*.



inside each cage (F1, one-year generation time). Because no trees died in the winter of 2014/2015, we did not assess trees the following winter. We assessed trees monthly from May to August in 2016. In November 2016, we conducted a final assessment of tree mortality and *S. noctilio* adult emergence holes inside each cage (new holes = F1, two-year generation time).

More trees were attacked and subsequently died when exposed to a high versus low density of *S. noctilio*. This is consistent with our a priori prediction at the outset of the study and observations that larger, more well-defended trees were attacked and killed most frequently at the peak of an outbreak (Madden 1975). Specifically, 78% of trees in the high-density treatment were attacked and killed by *S. noctilio*; 44% of trees in the low-density treatment were attacked and 33% were killed by *S. noctilio* (Fig. 1). Attack failure was more likely to occur in the low-density treatment (Fig. 1). If attacked, most trees eventually died and produced a F1 cohort, regardless of *S. noctilio* density (seven of seven in the high-density trees and three of four in the low-density trees).

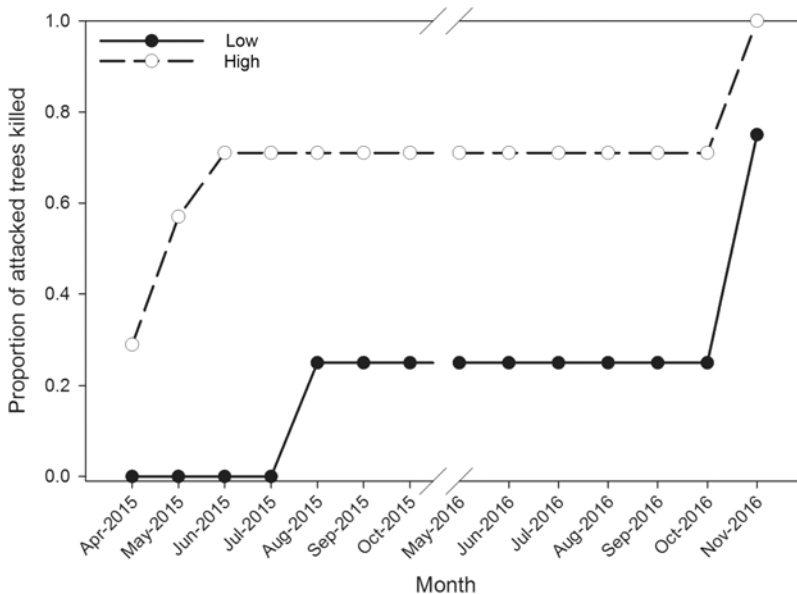
Our limited sample size prevents robust estimation of the frequency with which attack from a low-density *S. noctilio* population results in tree mortality. Observations indicate that the *S. noctilio* population is low in most Ontario pine forests, and trees were often attacked in several successive years before they died (Dodds *et al.* 2010; Haavik *et al.* 2018). Consistent with that, trees attacked by a high density of *S. noctilio*

died more rapidly than trees attacked by a low density of *S. noctilio* (Fig. 2). If attacked, most trees in the high-density treatment died the spring after attack; most in the low-density treatment died by the following fall, more than two years after attack (Fig. 2). A previous study in Ontario at sites with high *S. noctilio* populations found that pines naturally attacked by *S. noctilio* died between two weeks and seven months (the next spring) after attack (Ryan *et al.* 2013), which was similar to observations from *S. noctilio* populations on other invaded continents (Madden 1988).

In the high-density treatment, tree death was synonymous with production of a *S. noctilio* F1 cohort. Trees that died within one year (2015) produced a F1 cohort with a one-year generation time; trees that died the following year (2016) produced a F1 cohort with a two-year generation time. Of the four trees that were attacked by *S. noctilio* in the low-density treatment, none produced a F1 cohort with a one-year generation time, although one died within one year of attack. Variable development time, between one and three years, occurs in *S. noctilio* populations on other continents, is thought to be related to temperature, and can affect population growth, interactions, and synchronicity with natural enemies, as well as life history characteristics (Corley and Villacide 2012). Our results suggest that attack density is an additional factor that may contribute to variation in development time in *S. noctilio*.

Patterns in the high-density treatment were clear: most trees were attacked by *S. noctilio*,

Fig. 2. Cumulative proportion of trees that were attacked by *Sirex noctilio* that died by month, categorised by *S. noctilio* density (low = two mating pairs; high = 15 mating pairs). No trees in the study died prior to April 2015.



and if so, they subsequently died and produced a F1 cohort with a generation time consistent with time of *P. sylvestris* mortality, usually within one year of attack. Patterns in the low-density treatment were less clear: nearly half of the trees were attacked, and of those only half died and produced F1 *S. noctilio* within two years. Though our results were limited and require further investigation, they support existing literature and observations that suggest insect population density affects the likelihood of successful host colonisation by wood-boring insects. This has implications for future invasions of *S. noctilio* and other wood-boring insects and provides further evidence that size of the founding population affects the likelihood of establishment of an insect in a new range (e.g., Beirne 1975; Grevstad 1999).

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