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Sirex nigricornis (Hymenoptera: Siricidae) Larval Development Correlated with Tree Characteristics and Ophiostomoid Fungal Infection

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Abstract

The native North American woodwasp, *Sirex nigricornis* F. (Hymenoptera: Siricidae), has received significant attention over the last several years due to the introduction and successful establishment of the European woodwasp, *S. noctilio* F. in eastern North America. Larval size and development of *S. nigricornis* are important variables that can help to compare demography of the two species and predict future interactions. We measured head capsule width, body length, and weight of *S. nigricornis* larvae removed from 14 pine trees, felled across the Ozark and Ouachita National Forests of Arkansas in 2012. We also recorded the height at which larvae were removed, and the diameter of the stem at that height. We used logistic regression to compare proportions of larvae removed from each section of each tree. Two-thirds of the larvae collected came from a single tree. Most larvae were in the lower and middle sections of trees and larval size was positively correlated with tree diameter. Ophiostomatoid fungi were absent in trees that produced the highest number of larvae, implying *S. nigricornis* colonized those trees before bark beetles. These results have implications for interspecific competition and interactions among *S. nigricornis* and *S. noctilio,* and for management which relies on successful larval development to transmit parasitic nematodes.

Keywords: ***Sirex*****,** ***Ophiostoma,*** **invasive species**

Over the last several years, *Sirex nigricornis* F. (Hymenoptera: Siricidae) has received significant attention due to the North American introduction and establishment of *S. noctilio* F., a globally invasive pest (e.g. Hajek et al. 2013, Chase et al. 2014, Hartshorn et al. 2016b). The interactions among *S. noctilio, S. nigricornis*, and other pine-inhabiting insects, as well as their associated fungi, are important from an ecological standpoint; fewer native woodwasps and associates are found in trees infested by *S. noctilio* (Ryan et al. 2012). Their interactions are also important from a management stand point. A parasitic nematode native to North America, *Deladenus proximus* Bedding, has been able to colonize *S. noctilio* as a host and infect its eggs and mycangia (Yu et al. 2011, Morris et al. 2013). Fungal competition among the *Sirex* symbiont, *Amylostereum* Boidin (Russulales: Amylostereaceae), and bark beetle transmitted *Ophiostoma* Syd. & P. Syd., as well as tree defenses, have been implicated in *S. nigricornis* and *S. nocilio* egg and larval mortality (Haavik et al. 2015). While *A. areolatum* (Chaillet ex. Fr.) Boidin is associated with *S. noctilio* and *A. chaillettii* (Pers.) Boidin is associated with *S. nigricornis*, both woodwasp species are able to use both fungal species in development (Hajek et al. 2013). Both fungal species are easily outcompeted by bark beetle-associated ophiostomoid fungi which is likely due to the rapid decline in tree moisture content following infection (Ryan et al. 2011, Hubbard et al. 2013).

Understanding *Sirex* larval development is important in predicting how these species may interact in the future, relating to spread of *S. noctilio* into the "wood basket" of the southeastern United States. Spatial niche partitioning (e.g. Paine et al. 1981) is common among wood-boring insects as is significant size variation which is likely due to low mobility of wood-boring larvae, as well as host nutritional quality (Andersen and Nilssen 1983). Comparisons among size variation and larval development of *S. nigiricornis* and *S. noctilio* may assist in making management decisions in areas where the two species will overlap.

Both *Sirex* and associated parasites, namely *Deladenus* nematodes (Tylenchida: Neotylenchidae), utilize a symbiotic fungus, *Amylostereum* for development within the tree (Madden 1981, Yu et al. 2011). The nematode feeds directly on the fungus while free-living in the tree. *Sirex* larvae utilize specialized mandibles and N-fixing gut bacteria to extract nutrients and sugars from partially-degraded wood just behind the *Amylostereum* growth front (Thompson et al. 2014). Both *S. nigricornis* and *S. noctilio*, as well as multiple species of *Deladenus*, are able to develop on different species of *Amylostereum* (Hajek et al. 2013). Their reliance for development on a symbiotic fungus suggests that competition with other tree-inhabiting fungi, like *Ophiostoma*, may negatively affect both the woodwasp and its associated parasites (Yousuf et al. 2014, Yousuf et al. 2018). Species of *Ophiostoma* are commonly encountered fungi in pines in the United States that cause "bluestain" and are vectored by bark beetles (Coyle et al. 2016). Competition between these two fungal groups is likely affected by which insect species arrives at the tree first and this likely affects larval development, adult emergence, and therefore, future populations.

Our objective was to quantify the effects of tree height, diameter, and infection by ophiostomatoid fungi on larval development by examining number and size of larvae along the length of whole trees that were felled and left in the field for a year. We predict that, due to niche partitioning and intraspecific competition, more larvae will be present in the lower section of the tree where a larger diameter may support more larval development. We also predict that colonization by ophiostomatoid fungi will result in fewer developing larvae due to competition with *Amylostereum*.

Materials and Methods

In August 2010, eight loblolly pine (*Pinus taeda* L.) and six shortleaf (*Pinus echniata* Mill.) trees were felled in the Ozark and Ouachita National Forests in Arkansas and held in the field until July 2011 at which time they were returned to the lab, cut into 95 1-m long bolts (logs) up to a diameter of 12.7 cm, and split into slabs (slices) using a band saw and hatchet. Wood slabs were then dissected using a chisel. All larvae found during dissections were collected and head capsules (mm) and body length (cm) measured using calipers. Diameter (cm) was measured for each bolt, and height position along the bole was recorded as low (L), middle (M) or high (H) by dividing the total length of each tree into thirds. Presence of ophiostomatoid fungi (0 = absent, 1 = present) was also recorded for each bolt by visual confirmation of staining.

To determine effects of ophiostomatoid fungi on larval development, multiple regression was used with presence of fungi as the independent variable and total number of larvae as well as proportion of larvae per bole height (L, M, H) as dependent variables. To establish whether height along the bole (L, M, H) affected larval survival, a binomial regression with a logit link function (Whitlock and Schluter 2015) was created with height as the independent variable and proportion of larvae in each section as the dependent variable. Proportion of larvae was calculated by dividing the number of larvae from each section by the total number of larvae per tree. To quantify the effects of bole diameter on larval size, a Pearson's product-moment correlation test was used to calculate the correlation coefficient between body length and head capsule (0.68). Because the two size factors were significantly correlated (t = 12.948, $P < 0.0001$), a single linear model was created with log head capsule width as the response variable and diameter as the independent variable. All analyses were performed in RStudio (RStudio Team 2020).

Results

A total of 201 larvae across 14 trees was collected. All larvae were late instars, and appeared to be of a single cohort. Of the 14 trees that were felled, eight contained bolts with ophiostomatoid fungi. In trees with the fungus, it was present throughout nearly the entire bole. *Ophiostoma* did not significantly affect the proportion of *S. nigricornis* larvae in each section ($F = 0.006$, $P = 0.936$) but it did significantly affect the total number of larvae collected ($F = 7.122$, $P = 0.0109$). The vast majority of *S. nigricornis* larvae (168; 84%) were collected from trees that did not contain ophiostomatoid fungi.

Of the 201 total larvae, 133 (66%) were removed from a single tree collected from the Ouachita National Forest. Significantly more *S. nigricornis* larvae were found in the lower and middle sections of the trees ($F = 6.013$, $P = 0.0053$; Table 1) and head capsule width of *S. nigricornis* larvae was significantly positively affected by tree diameter ($F = 8.858$, $P = 0.0033$; Fig. 1).

Discussion

Our prediction of more larvae in the lower section of the tree was validated. However, a third of all *S. nigricornis* larvae collected were from a single tree, which makes extrapolation across trees difficult. These results do, however, fit with previous studies showing *S. noctilio* attack distribution to be highly aggregated in a few trees within stands (Lantschner and Corley 2015). While *S. nigricornis* attacks do not produce

Table 1. Characteristics of trees collected for dissection.

Tree #	Location	# Bolts	Total Height (m)	DBH (cm)	Species	# *Sirex* larvae	*Ophiostoma* (%)
1	Ouachita NF	6	6	30.5	Loblolly	2	0
2	Ouachita NF	8	8	35.5	Loblolly	133	0
4	Ouachita NF	7	7	16	Loblolly	2	100
64	Ouachita NF	5	8.8	21.2	Loblolly	2	50
66	Ozark NF	5	5.25	45.2	Shortleaf	1	100
67	Ozark NF	5	5.25	26.7	Shortleaf	3	100
68	Ouachita NF	8	11.9	28.5	Loblolly	4	100
69	Ouachita NF	10	14.6	34.3	Loblolly	15	100
71	Ouachita NF	7	11	27.9	Shortleaf	3	33
72	Ozark NF	5	5.25	26.3	Shortleaf	3	100
74	Ozark NF	7	9.5	25.4	Shortleaf	2	0
75	Ozark NF	5	8	28.5	Shortleaf	2	0
76	Ouachita NF	5	8.8	26.7	Loblolly	6	0
77	Ouachita NF	12	16.2	31.2	Loblolly	23	0

resinosis as do *S. noctilio* attacks (Ryan et al. 2013), previous studies have found that females strongly prefer fresh trees but development is highest in trees with moderate moisture loss (Hartshorn et al. 2016a). Individual trees serving as the main reservoir for developing *Sirex* larvae implicates between-tree variation in variables such as moisture and tree defenses, as a major driver of larval development and survival. This has been found for *S. noctilio* natural and lab-reared cohorts (Haavik et al. 2016). Based on previous studies looking at *S. nigricornis* oviposition preferences related moisture loss in pines (Hartshorn et al. 2016a), the aggregation found in this study suggests that the trees with the highest number of larvae were those with moderate moisture stress, likely related to ophiostomoid fungal infection associated with bark beetle infestation (Hubbard et al. 2013).

Ophiostomatoid fungi were found in eight of the 14 total trees, and across nearly the entire bole of those eight trees (Table 1). Research has investigated interactions among *Sirex* and wood-boring beetles, with fungal competition appearing to play a major role (Hurley et al. 2012). Competition among *Amylostereum* and *Ophiostoma* has implications for larval development (Thompson et al. 2014) as well as management in that the parasitic nematode used in biological

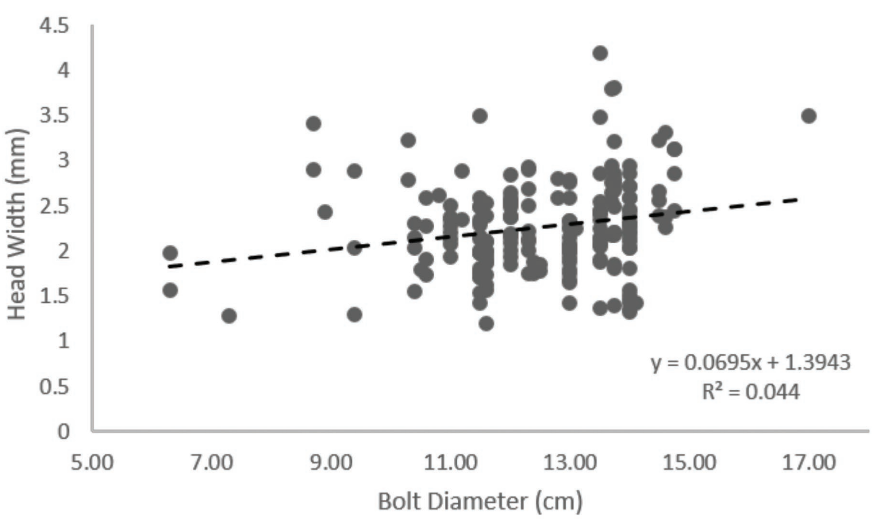

Figure 1. Linear model of larval head capsule width across bolt diameter with equation and R^2 reported.

control of *S. noctilio, Deladenus siricidicola* Bedding, feeds on *Amylostereum*. Due to this reliance on *Amylostereum,* the development of both the woodwasp and nematode may be hindered in the presence of ophiostomatoid fungi (Yousuf et al. 2018). Because our trees were left in the field for nearly a year, all larvae collected were late-instar and represent a final natural cohort. Based on fungal competition studies, we can infer that *S. nigricornis* was the first insect to arrive at trees with the most successful larval development. On the trees infected with ophiostomatoid fungi, bark and ambrosia beetles likely arrived prior to *S. nigricornis*.

Significantly more larvae were found in the lower and middle sections of the tree compared to the top sections. This contrasts with studies that have found consistent emergence along the length of the bole with no effect of height, although more, and larger, *S. noctilio* were found in larger trees (Ryan et al. 2012). In our study, larvae were significantly larger in the lower sections of the tree. Most mortality of *S. noctilio* occurs during the egg and neonate stage (Haavik et al. 2015) and we assume this to be true for *S. nigricornis* as well. Host preference tests have shown that *S. noctilio* prefers the European species, Scots pine (*P. sylvestris* L.) but will drill into, and emerge from, North American pines such as red pine (*P. resinosa* Aiton) Virginia pine (*P. virginiana* Mill.) and eastern white pine (*P. strobus* L.) (Dinkins 2011). However, no adults emerged from Loblolly pine (*P. taeda*) in their study.

Our results suggest that larval survival is highest in the middle section of trees without ophiostomatoid fungal infection which also suggests that survival is highest in trees where *S. nigricornis* is the first insect to colonize the tree. These results support studies on *S. noctilio* and imply that interspecific competition will minimize spread of *S. noctilio* into the southeastern United States. Interspecific competition is likely among these groups as it is most common in sessile, aggregated, introduced insects (Denno et al. 1995). Demography and within-tree interactions among the two species, as well as other wood borers, warrant investigation to elucidate potential future impacts of *S. noctilio* spread.

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