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Jeremy D. Allison, Bernard Slippers, Marc Bouwer & Brett P. Hurley

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Simulated leks increase the capture of female *Sirex noctilio* in the absence of host volatiles

Jeremy D. Allison^{a,b} (b), Bernard Slippers^c (b), Marc Bouwer^d (b) and Brett P. Hurley^b (b)

^aGreat Lakes Forestry Centre, Natural Resources Canada-Canadian Forest Service, ON, Canada; ^bDepartment of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Gauteng, South Africa; ^cDepartment of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Gauteng, South Africa; ^dDepartment of Chemistry, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Gauteng, South Africa

ABSTRACT

Male *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) form leks in the upper canopy where mating occurs and have an orange abdominal segment not present in females. This study used field trapping studies in South Africa to examine the impact of stimuli (primarily visual) associated with male *S. noctilio* on the capture of conspecific females. Although we observed that traps baited with dead males (simulated leks) captured more females than unbaited traps, traps baited with a synthetic blend of host volatiles captured more female *S. noctilio* than traps baited with dead males. Additionally, dead males provided no additive effect on trap catch when combined with the host volatile lure regardless of the simulated lek size or if males were alive or dead. These results are the first to experimentally confirm an effect of a conspecific, and potentially mating related, visual stimulus on the behavior of *S. noctilio*. There appears to be limited potential for improvement of existing *S. noctilio* trapping methods by the addition of male decoys as deployed in this study.

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Introduction

The ability to detect and monitor invasive forest insect pests is key for the development of management strategies targeting them (Brockerhoff et al. 2006; Poland and Rassati 2019). Effective survey and detection tools can be used to detect new or spreading populations of invasive insects quickly and the sooner after invasion detection occurs the smaller the infested area is likely to be and the more likely it is that eradication efforts will be successful (Brockerhoff et al. 2010). Similarly, these same tools can be used to monitor populations of established invasive insect pests and provide data to assess and implement management strategies (Bashford 2008). These survey and detection tools can also be used to evaluate the impact of management activities. Traps baited with olfactory and visual attractants are a common tool used for survey and detection of insects (Poland and Rassati 2019), particularly for bark beetles and wood-boring insects (Allison et al. 2001; McIntosh et al. 2001; Bashford 2008; Bouwer et al. 2017).

The primary modalities exploited for the development of survey and detection tools are olfaction and vision. For example, black multiple-funnel traps are frequently used to detect and monitor

coniferophagous beetles. These traps are often baited with pheromone or plant volatile lures serving as an olfactory attractant for the insect, and the vertical silhouette of the trap simulates the host tree (Campbell and Borden 2006a, 2006b). Visual cues used in traps can also be in the form of decoys of the target insect, as has been tested with the emerald ash borer, Agrilus planipennis Fairmaire (Coleoptera: Buprestidae) (Lelito et al. 2008; Domingue et al. 2013). In many cases insects integrate both visual and olfactory information (Baker and Hansson 2016). All three bark beetle species tested by Campbell and Borden (2006a) preferred attractantbaited traps that visually simulated the host tree as opposed to the same traps that did not (hosts were simulated visually by manipulating trap color). The relative importance of visual and olfactory stimuli differs between species (Kerr et al. 2017).

Semiochemical-baited traps are an important tool to detect and monitor populations of the European woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), in its invasive range. This insect is native to Eurasia and North Africa, but was unintentionally introduced throughout the pine growing regions of the southern hemisphere in the 1900s where it has become a serious pest in pine plantations (Hurley et al. 2007). More recently it has been introduced in

CONTACT Jeremy D. Allison 🛛 jeremy.allison@canada.ca 🖃 Canadian Forest Service Great Lakes Forestry Centre 1219 Queen Street East Sault Ste. Marie ON P6A 2E5 Canada

North America (Hoebeke et al. 2005; de Groot et al. 2006) and China (Li et al. 2015). In the southern hemisphere, semiochemical-baited traps have been used to monitor the spread of established populations into new areas and inform management decisions (Bashford 2008; Hurley et al. 2012). In particular, annual inoculations of the nematode Deladenus siricidicola Bedding (Tylenchidaa: Neotylenchidae) (Bedding and Akhurst 1974), the primary biological control agent for S. noctilio are focused in sites of new or increasing infestation (Hurley et al. 2012). Currently no operational monitoring occurs for S. noctilio in North America, but research trials examined the use of stem injections to create trap trees (Zylstra et al. 2010) and compared semiochemical-baited panel and multiplefunnel traps (Haavik et al. 2014).

Black panel or multiple-funnel traps baited with a synthetic blend of plant volatiles are the dominant traps currently used to detect and monitor populations of S. noctilio (Dodds and de Groot 2012; Hurley et al. 2015). These traps have been relatively successful with moderate to high populations, but are often not effective in low populations, especially when surrounded by host trees producing competing volatiles (Crook et al. 2012; Dodds and de Groot 2012; Haavik et al. 2014). The host volatiles used are also not specific and attract many other insect species (Olivier-Espejel et al. 2017), making sorting through trap collections an expensive and timely process (Dodds and de Groot 2012). In addition to the attractive effects of the host volatile lure, the shape of the trap mimics the host tree bole/ silhouette and presents additional cues to attract wasps (Sarvary et al. 2015), but this is also not specific to S. noctilio. Contact pheromones exist (Böröczky et al. 2009), as well as a putative volatile pheromone (Cooperband et al. 2012), but it has not proven effective in the field (Hurley et al. 2015; Sarvary et al. 2015).

In taxa that use visual cues and signals in mate location, these may be used to develop survey and detection tools, as has been shown with A. planipennis (Domingue et al. 2013). Sirex noctilio has a male biased sex-ratio (Ryan and Hurley 2012; Queffelec et al. 2019). Males emerge first and gather in the upper branches of trees where they form leks and are joined by females (Madden 1988). It has been hypothesized that a male produced pheromone attracts both sexes to leks (Cooperband et al. 2012) and monoalkenes on the cuticle of the female act as contact sex pheromones (Böröczky et al. 2009). Sirex noctilio are sexually dimorphic with males having an orange abdominal segment not present in females (Madden 1988). This suggests that male wasps may provide a visual signal that contributes to mate finding, although Caetano and Hajek (2017)

observed that in the lab males approached females from behind to initiate mating.

We examined the impact of stimuli (primarily visual) associated with male *S. noctilio* on female *S. noctilio* trap captures. Black panel traps placed in the field were used in three experiments to compare trap catch: 1) in the absence/presence of dead males; 2) between different simulated lek sizes (number of males); and 3) with and without male olfactory stimuli of the male wasp. The first experiment included treatments with and without the addition of the synthetic host volatile lure, however, because of the strong effect of the synthetic host volatile, all treatments for the subsequent two experiments included the host volatile.

Methods

Three field trapping experiments were conducted in a Pinus patula Schiede ex Schltdl. & Cham (Pinales: Pinaceae) plantation in Mpumalanga near Carolina, South Africa. In experiment 1, a 2×2 factorial design was used to look at the effect of the presence/absence of visual (4 dead male S. noctilio tethered to the trap) and olfactory (synthetic host volatile lure) stimuli on the capture of female S. noctilio. Experiment 2 examined the effect of simulated male lek size (0, 4, 8, and 16 dead male S. noctilio tethered to the trap) on the capture of female S. noctilio. Experiment 3 looked for evidence that male S. noctilio present olfactory stimuli in addition to visual stimuli that may influence the capture of female S. noctilio. This was done by manipulating the potential for males to present olfactory stimuli.

Male S. noctilio used to create trap treatments in all three experiments were obtained from infested logs collected near Carolina, Mpumalanga, South Africa just prior to wasp emergence. Logs were placed in emergence cages in an insectary and wasps were used within 3 days of emergence. Intercept panel traps with bottom collection containers designed for wet trapping (Insect Science, Tzaneen, South Africa) were used in all three field trapping experiments. Water was placed in the collecting containers, to about one quarter of the container height, and a small amount of scentless dish detergent was added to reduce surface tension. The water and dish detergent were replaced at each trap collection. Traps were hung on trees such that the bottom of the trap was ca. 1.8 m above the ground.

For the host volatile treatment, a Sirex Pherolure (Insect Science, Tzaneen, South Africa) was hung in the centre of the cut-out bait area of the panel trap (Experiment 1: treatments 2 and 4; Experiments 2 and 3: all treatments) (this lure has been described in more detail by Hurley et al. (2015)). All three

trapping experiments included four treatments and traps were deployed in a 4×10 grid, maintaining a distance of ca. 30 m between traps and no trap was hung from a tree within 30 m of a compartment edge. In all three experiments the first trap location within the first replicate block received treatment 1 and subsequent treatments were assigned to traps sequentially (i.e. trap 2 within the first replicate block had treatment 2). In each subsequent replicate block within each experiment, treatments were shifted one position (i.e. the first trap of the second replicate block received treatment 4, the second trap received treatment 1, the third received treatment 2 and the fourth trap received treatment 3).

Experiment 1, conducted in 2014, compared the capture of female S. noctilio in: 1) unbaited panel traps; 2) traps baited with synthetic host volatiles; 3) traps baited with a simulated lek of four dead male S. noctilio; and 4) traps baited with both synthetic host volatiles and a simulated lek of four dead male S. noctilio. The rationale behind this experiment was that S. noctilio is sexually dimorphic with males having a highly conspicuous band of orange coloration on the abdomen that is absent in females and form leks where mating occurs (Madden 1988). Live male S. noctilio were placed overnight in a freezer and subsequently thawed and ca. 50 cm of 15-pound test fishing line was attached to the dorsal surface of the thorax with a hot glue gun. One male was hung from the top corners (4 per trap for treatments 3 and 4) of each trap such that males hung down to the ca. middle of the trap. Damaged and missing males were replaced as needed at each collection event (this was rare and never more than 1 male per block).

Experiment 2, conducted in 2015, compared the capture of female S. noctilio by traps baited with: 1) synthetic host volatiles (HV); 2) HV plus 4 dead males; 3) HV plus 8 dead males; and 4) HV plus 16 dead males. The rationale behind this experiment was that the size of the male lek may influence the attraction of female S. noctilio. Tethered males were created using the methodology developed and described in Experiment 1 above. Zero, 1, 2 and 4 males were hung from the top corners of each trap to create traps with simulated lek sizes of 0, 4, 8 and 16 males (i.e. treatments 1-4). To minimize the potential for tethered males to become tangled and damaged in treatments 3 and 4, males were hung 1 and 3 cm from each corner in treatments 3 and 4. Damaged and missing males were replaced as needed at each collection event (this was rare and never more than 1 male per block).

Experiment 3, conducted in 2015, compared the capture of female *S. noctilio* in traps baited with: 1) synthetic host volatiles (HV); 2) HV plus 4 fresh dead males; 3) HV plus 4 solvent extracted and dried dead males; and 4) HV plus 4 live males.

The rationale behind this experiment was that a male-produced volatile sex pheromone has been reported for *S. noctilio* (Cooperband et al. 2012) but it has not been effective in field trapping studies (Hurley et al. 2015). If female response to the pheromone is context-dependent there may be synergism between olfactory and visual stimuli associated with male *S. noctilio*. Live males could present both visual and olfactory (e.g. pheromones) stimuli; fresh dead males would present visual stimuli, but would be less likely to present olfactory stimuli and the solvent extracted and dried males would only present visual stimuli.

The fresh dead males in treatment 2 were created and deployed from traps as described above in Experiment 1. The males from treatment 3 were immersed for 30 min 10 males/beaker in ca. 25 ml hexane and then dried for 18h in a drying oven (70°C, 1400 W Memmert). Dried males then had fishing line attached to their thorax as described above. The day before deployment in the field, live males were immobilized by placing them in a beaker in an ice bath for a few minutes. Males were removed from the ice bath and had fishing line attached to their thorax as described above. To keep males from damaging and/or freeing themselves from their tether, tethered males were kept in a chilled cooler overnight until they were deployed in the field. In treatments 2, 3 and 4, males were hung individually from the top corners (4 per trap) of each trap such that males hung down to the ca. middle of the trap. Damaged and missing males were replaced with an appropriate male as needed at each collection event (this was rare and never more than 1 male per block).

The experimental designs were identical for all three field trapping experiments and consequently so were the statistical analyses. Captures of female S. noctilio were summed across all collection dates for analysis. Total trap captures of female S. noctilio were analyzed using a blocked multi-response permutation procedure (McCune and Grace 2002). All analyses were conducted with PC-ORD 6.0 (MjM Software Design, Gleneden Beach, OR, USA) using Euclidean distances to construct the distance matrix with blocks aligned before analysis (McCune and Grace 2002) and the multiplicity effect was conusing step-up False Discovery trolled Rate (Benjamini and Hochberg 1995; Garcia et al. 2004).

Results

Experiment 1: Presence/absence of olfactory and visual stimuli

A total of 1116 female *S. noctilio* were captured and a significant treatment effect was observed (T = -10.44; p < 0.001) in this experiment. Traps



Figure 1. Mean total capture (+SE) of female *Sirex noctilio* in panel traps in Experiment 1. Traps were equipped with wet cups and either unbaited blank controls or baited with a synthetic blend of host volatiles (HV) (Sirex Pherolure, Insect Science), a simulated lek of 4 fresh dead male *S. noctilio*, or both HV and a simulated lek of four fresh dead male *S. noctilio*. There were 10 replicates per treatment. Means (+SE) followed by the same letter are not significantly different at p = 0.05.

baited with synthetic host volatiles, simulated male leks, and both synthetic host volatiles and simulated male leks, all captured significantly more female *S. noctilio* than unbaited traps (Figure 1). Traps baited with synthetic host volatiles alone or baited with synthetic host volatiles and simulated male leks both captured significantly more female *S. noctilio* than traps baited with simulated male leks alone. There was no significant difference in the number of female *S. noctilio* captured by traps baited with synthetic host volatiles alone or traps baited with synthetic host volatiles and simulated male leks.

Experiment 2: Male lek size *and* **Experiment 3: Potential for male olfactory stimuli**

A total of 312 and 440 female *S. noctilio* were captured in experiments 2 and 3, respectively. In both experiment 2 (T = -0.40; p = 0.28; Figure 2) and experiment 3 (T = 0.46; p = 0.62; Figure 3) there was no treatment effect. In experiment 3 all live males for treatment 4 were replaced after the first collection, but not the second and no males were observed to survive the entire week between deployment and collection. This means that at the start and finish of the last collection, none of the males in treatment 4 were alive. Of the 440 female *S. noctilio* captured over the three collections, only 35 came from the third collection. The data from this experiment were analyzed with and without the third collection and qualitatively the results were the



Figure 2. Mean total capture (+SE) of female *Sirex noctilio* in panel traps in Experiment 2. Traps were equipped with wet cups and baited with a synthetic blend of host volatiles (HV) (Sirex Pherolure, Insect Science) or HV and a simulated lek of 4, 8 or 16 fresh dead male *S. noctilio*. There were 10 replicates per treatment. There were no significant treatment effects.



Figure 3. Mean total capture (+SE) of female *Sirex noctilio* in panel traps in Experiment 3. Traps were equipped with wet cups and baited with a synthetic blend of host volatiles (HV) (Sirex Pherolure, Insect Science) or HV and a simulated lek of male *S. noctilio*. The simulated male leks either had four fresh dead males, four dead males extracted in hexane and dried or four live males. There were 10 replicates per treatment. There were no significant treatment effects.

same. The data from the third collection were included in the final analyses.

Discussion

This study observed higher numbers of female *S. noctilio* in traps baited with dead male *S. noctilio*

than in unbaited traps; however, traps baited with male wasps captured significantly fewer wasps than traps baited with the host volatile. Simulated male leks also provided no additive effect on trap catch when combined with the host volatile. This was true for the different lek sizes tested and for the use of live and dead male wasps to simulate leks. These results suggest limited or no potential to use visual stimuli (male decoys) to increase the performance of existing survey and detection tools (host volatile baited traps) for *S. noctilio*.

To locate resources (e.g. mates, prey, host plants) insects should perceive and respond appropriately to stimuli (signals and cues) from multiple modalities. This study confirms the role of both conspecific visual and host olfactory stimuli in behavioral responses in S. noctilio. Numerous studies have demonstrated effects of olfactory and visual stimuli on the capture of forest insects (Lanier 1983; Allison et al. 2004, 2013; Strom et al. 1999, 2001; Campbell and Borden 2006a, 2006b, 2009; Allison and Redak 2017) but little is known about the effect of visual and olfactory stimuli and the relative contribution of these to mate and host location in wood-boring hymenoptera. Campbell and Borden (2009) reported that the response of Urocerus gigas flavicornis (Fabricius) to host volatiles was influenced by visual stimuli but that no effect of visual or olfactory host stimuli was observed in Xeris spectrum (Linnaeus).

Host related olfactory cues had a stronger effect on S. noctilio behavior than the visual stimuli from male wasps presented in this study. The relative contribution of each sensory modality should be determined by stimulus apparency, reliability and costs of using the associated sensory modality (Pyke et al. 1977; Fawcett and Johnstone 2003). The stimuli and sensory modalities used vary among species. For example, Kerr et al. (2017) compared the effect of visual (trap color) and olfactory (attractants and repellents) stimuli on the trap catch of two bark beetle species, Hylurgus ligniperda(Fabricius) (Coleoptera: Curculionidae) and Hylastes ater (Paykull) (Coleoptera: Curculionidae), and one longhorn beetle, Arhopalus ferus (Mulsant) (Coleoptera: Cerambycidae). Visual cues had the strongest effect on trap catches of H. ater and A. ferus, but olfactory cues had the strongest effect on trap catches of H. ligniperda.

A number of factors that could influence response to olfactory and visual cues were not considered in this study and could be considered in future studies. For example, responses to olfactory and visual stimuli have been reported to vary within species. The effect of trap color on the coffee berry borer, *Hypothenemus hampeii* (Ferrari) (Coleoptera: Cerambycidae) varies depending on the release rate of host-associated volatiles (Mathieu et al. 1997). In addition, synergism of responses to host cues when cues from multiple sensory modalities are presented, has been reported (Henneman et al. 2002; Raguso and Willis 2005), including the responses of insect herbivores (Judd and Borden 1991).

The stronger responses to olfactory rather than visual stimuli and absence of an additive effect of the visual stimuli when olfactory cues were present that were observed in our study could be related to the mating and host location behavior of S. noctilio. Male leks occur in the upper branches of the tree and consist of unmated males and females (Madden 1988). Within leks, olfactory stimuli from male wasps (Böröczky et al. 2009; Cooperband et al. 2012) and possibly visual stimuli from males/the male lek, likely mediate mate location. Less clear is the role that olfaction and vision play in female S. noctilio location of male leks. A volatile maleproduced pheromone has been reported in S. noctilio (Cooperband et al. 2012). Although this putative mating signal could mediate upwind orientation of female S. noctilio to male leks, field trials have not observed an effect on female trap capture (Hurley et al. 2015; Sarvary et al. 2015).

Our traps were placed at ca. 1.8 m above ground and may have been too low in the understorycanopy gradient to attract mate-seeking female S. noctilio. Hurley et al. (2015) compared trap catches of S. noctilio at different heights, using the same traps utilized in this study, but baited with the putative male-produced aggregation pheromone (Cooperband et al. 2012). In that study higher traps caught only marginally more wasps, but it is possible that trap height could have a stronger influence on the visual cues from the male wasps. Martínez et al. (2014) also observed that male S. noctilio fly higher than females and when males were present on sticky mesh traps females were reported to fly higher than in the absence of males. The authors suggested that this behavioral variance was most likely due to females searching for mates and oviposition substrates at different heights. It is possible that while both olfactory and visual stimuli may mediate host and mate location by S. noctilio they may do so at different levels of the understorycanopy gradient. Field trapping studies on other insects have also demonstrated that trap location along horizontal edge-interior (Allison et al. 2019) and vertical understory-canopy (Rassati et al. 2019) forest gradients can have a significant effect on captures of woodboring insects.

Future work on the visual ecology of *S. noctilio* woodwasps should consider where stimuli should be presented in the understory-canopy gradient. It is also possible that the effect of trap location on the

understory-canopy gradient is not linear and no effect of trap height may be observed until traps are above a threshold. In this scenario all traps below this unknown threshold would capture similar numbers, and only if traps were simultaneously deployed above and below the threshold would an effect of trap height be observed. Consequently, the putative pheromone and visual lek signals would only increase trap capture if they were deployed above the response threshold height. However, the feasibility of using traps placed high in the canopy for wide scale monitoring would need to be considered. It is thus possible that deployment of traps that simulate the visual and/or olfactory cues that S. noctilio uses in host location will remain the most feasible approach for monitoring this insect pest. Furthermore, recent work that has shown that female S. noctilio are attracted to volatiles produced by its fungal symbiont, Amylostereum areolatum (Fernández Ajó et al. 2015; Sarvary et al. 2016), should also be considered for its potential use in survey and detection of S. noctilio.

Disclosure statement

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ORCID

Jeremy D. Allison **b** http://orcid.org/0000-0002-0765-3149

Bernard Slippers (http://orcid.org/0000-0003-1491-3858 Marc Bouwer (http://orcid.org/0000-0002-0435-0919 Brett P. Hurley (http://orcid.org/0000-0002-8702-5547

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