2015

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Agricultural and Forest Entomology

Agricultural and Forest Entomology (2015), **17**, 29–35 DOI: 10.1111/afe.12077

The importance of olfactory and visual cues in developing better monitoring tools for *Sirex noctilio* (Hymenoptera: Siricidae)

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Abstract

1 To improve the monitoring of the invasive European woodwasp, both sexes of *Sirex noctilio* were studied in a walk-in wind tunnel. We evaluated three trap types: unbaited traps, traps baited with a three-component pheromone lure and traps baited with a commercial *Sirex* kairomone lure and ultraviolet light.

2 When no lure was present, the black intercept trap caught more females than the clear jar trap. The increase in pheromone concentration from 0.1 to 1 mg increased the capture of females, and not males, in the black intercept panel trap. Both of these findings suggest that the visual cues provided by the black intercept trap play an important role in attraction for females.

3 Capture rates between unbaited clear versus black intercept traps did not differ but the addition of a ultraviolet light increased trap efficacy. Intercept traps baited with light were more attractive than the commercial kairomone lure.

4 Both olfactory and visual cues were found to play important roles in the response of *S. noctilio* to traps. A black trap may enhance the capture of females, whereas the addition of ultraviolet light could enhance capture for both sexes. Integrating these different components may help in developing an improved species-specific trap for *S. noctilio*.

Keywords Insect detection, intercept trap, kairomones, olfactory cues, pheromones, phototaxis, visual cues.

Introduction

The European woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae) oviposits into healthy pine trees, depositing with the egg a symbiotic phytopathogenic fungus *Amylostereum areolatum* (Fr.) Boid. and a phytotoxic mucus, which cause the infected trees to eventually die (Coutts, 1969a,b). Over the last century, *S. noctilio* has been introduced to areas throughout the Southern Hemisphere with plantations of North American pine species and has caused extensive damage. For example, over 5 million Monterey pines *Pinus radiata* D. Don were killed between 1987 and 1989 during an outbreak in Australia (Haugen *et al.*, 1990; Ciesla, 2003). In North America, *S. noctilio* were first collected in New York, U.S.A., in 2004 (Hoebeke *et al.*, 2005), and Ontario, Canada, in 2005 (de Groot *et al.*, 2007). Laboratory studies using a flight mill have found that *S. noctilio* can fly a mean of 30.5 km in a 23-h time period (Villacide & Corley, 2008). Delimitation surveys began in the U.S.A., and, to date, *S. noctilio* has been found in seven states (New York, Pennsylvania, Michigan, Connecticut, New Jersey, Ohio, Vermont) (NAPIS, 2013). However, surveillance for *S. noctilio* in the U.S.A. has diminished in recent years and so its current distribution is likely underestimated (NAPIS, 2013).

Early detection of *S. noctilio* can be difficult as a result of low population densities and poor attraction to currently employed traps, which compete with surrounding host pine trees for gravid females (Crook *et al.*, 2012a). Signs of *Sirex*-infested trees used for visual inspection are subtle (Hoebeke *et al.*, 2005; Ayres *et al.*, 2009) and no *Sirex*-specific traps are currently available. Traps used to detect *S. noctilio* have been based on traps designed to catch other forest pests (intercept traps and funnel traps) baited with general kairomone attractants (Bashford, 2008; Dodds *et al.*, 2012; Hurley *et al.*, 2014).

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Because *S. noctilio* has become an important invasive pest in a number of countries, efforts to identify attractants have been made using electrophysiology, field studies and laboratory bioassays (Simpson, 1976; Simpson & McQuilkin, 1976; Cooperband *et al.*, 2012; Crook *et al.*, 2012a). Bashford (2008) conducted field studies in Tasmania aimed at developing a trap and lure for *S. noctilio* to detect new populations without the use of trap trees, ground surveys or aerial surveys. That study found that a 70/30 blend of α/β pinene attracted more *S. noctilio* than other ratios or either component alone. Hurley *et al.* (2014) reported that an α/β pinene blend has been augmented with several additional kairomone compounds and is commonly used for *Sirex* trapping in South Africa.

In the U.S.A., the Cooperative Agricultural Pest Survey is a national programme, involving federal and state agencies, cooperating in efforts to detect new invasions of pest species of concern. Their approved method for survey of *S. noctilio* has been the use of either black intercept panel traps, or black multi-funnel (8–12) Lindgren traps, baited with lures containing the 70/30 blend of α/β pinene (Bashford, 2008; Jackson *et al.*, 2012) and, generally, only females are trapped (K. Zylstra, personal communication). However, as a result of the low sensitivity of these traps and lures, visual inspection of trees is still considered one of the most reliable methods for the early detection of *S. noctilio* (Jackson *et al.*, 2012). Madden and Irvine (1971) and Madden (1971) found that girdled Monterey pine trees could be used to create trap trees for detection of *S. noctilio*. Trap trees have been integral in detection of *S. noctilio* in the Southern Hemisphere (Zylstra *et al.*, 2010; Bashford & Madden, 2012). The use of trap trees, however, is destructive, requires permission from tree owners, and is highly labour intensive. Therefore, traps baited with pine odours have been used for most *S. noctilio* detection in North America (Zylstra *et al.*, 2010; Jackson *et al.*, 2012), even though trap trees are considered more effective than traps baited with kairomones (Zylstra *et al.*, 2010).

Recently, an aggregation pheromone [100 : 1 : 1 ratios of (*Z*)-3-decenol, (*Z*)-4-decenol and (*E*,*E*)-2,4-decadienal] was described that attracted both male and virgin female *S. noctilio* in a laboratory wind tunnel (Cooperband *et al.*, 2012). Such an attractant offers the possibility of species-specific trapping. Additionally, a trap targeting males could enhance early detection because new invasions of *S. noctilio* are usually strongly male-biased (Ryan & Hurley, 2012). In wind tunnel bioassays, Cooperband *et al.* (2012) reported that, although both sexes were attracted to the pheromone, males engaged in different behaviours in the final stages of their approach compared with females. Males avoided contact with small pheromone-baited targets made out of black intercept trap material, whereas females landed on them. Although most *S. noctilio* studies have focused on using olfactory cues in trapping, these differences between the behaviours of males and females approaching the pheromone-baited target suggested that the use of visual cues in *S. noctilio* also needs to be examined. In addition to testing traps baited with the new pheromone for their ability to capture male and female *S. noctilio*, the present study also examined how *S. noctilio* males and females respond to traps with different visual cues such as transparent traps and ultraviolet (UV) light-baited traps.

Materials and methods

Insect rearing and mating

Sirex noctilio adults were reared from red pine (*Pinus resinosa* Sol. ex Aiton) and Scots pine (*Pinus sylvestris* L.) trees from infested areas of upstate New York and northern Pennsylvania. Felled trees with *Sirex* infestation symptoms (Ayres *et al.*, 2009) were cut into bolts approximately 1 m in length. Bolts were stored in an unheated structure at ambient temperatures in screen-covered fibre barrels (height 77.5 cm, diameter 51.4 cm). Barrels were almost always checked daily between 1 July and 30 September and all emerging woodwasps were collected. Adult *S. noctilio* were kept individually in 29.6-mL clear plastic cups (Solo Inc., Lake Forest, Illinois) containing a strip of dry paper towel at 4 °C for up to 3 weeks. Females were assumed to be virgins when collected from barrels with no males present, and virgin females were always used, except for experiments involving kairomone, which tested both virgin and mated females. Mating of *S. noctilio* females was visually observed in tent-like cages (width 61 cm, depth 61 cm, height 61 cm) (Bug Dorm 2; BioQuip Products, Rancho Dominguez, California) in which one female and 10 males were released. Mated wasps were stored at 4 °C for 24–72 h before they were used in flight studies.

Bioassay protocol

All flight studies were conducted under semi-field conditions, in a field wind tunnel (width 2 m, height 2 m, length 4 m) with polyethylene plastic sheet walls and ceiling (Husky clear 6 mil; Poly-America, Grand Prairie, Texas), similar to the wind tunnel used in Cooperband and Cardé (2006a). For experiments in 2011, the wind tunnel was assembled in a greenhouse at Cornell University with the upwind portion facing north. Experiments were conducted between 10.00 and 19.00 h. Natural light was used but without shading and *S. noctilio* flew directly to strong direct sunlight. Therefore, shades were arranged outside the wind tunnel to block the direct sunlight. Thus, mean light conditions were between 300 and 475 lux, measured using a light meter (LI-COR, Lincoln, Nebraska). The mean temperature during experiments was 28.4 °C (range 23–36 °C). Airflow was maintained using a fan (diameter 42 cm) (1/4 HP, 1725 r.p.m.; Dayton Electric, Niles, Illinois), which pushed air into the wind tunnel. Wind speed was frequently measured using a hot-wire anemometer (Testo Inc., Sparta, New Jersey) and wind velocity was maintained between 40 and 50 cm/s near the traps. The airflow was visualized using an airflow indicator smoke gun (Quickpoint Inc., Concord, Massachusetts). The wind tunnel was oriented such that air was vented out of the greenhouse to avoid recirculation into the tunnel. In the no-choice experiments in both years, a single trap was placed 1.5 m above ground, centered in the upwind end of the wind tunnel, and woodwasps were released approximately 3 m downwind of the traps.

In 2012, the same wind tunnel was used, although it was assembled inside a garage-like structure with artificial lights (the greenhouse was unavailable). To avoid recirculation of air, the fan drew fresh air in through an exterior door at the upwind end of the tunnel, and air leaving the tunnel was vented out the open

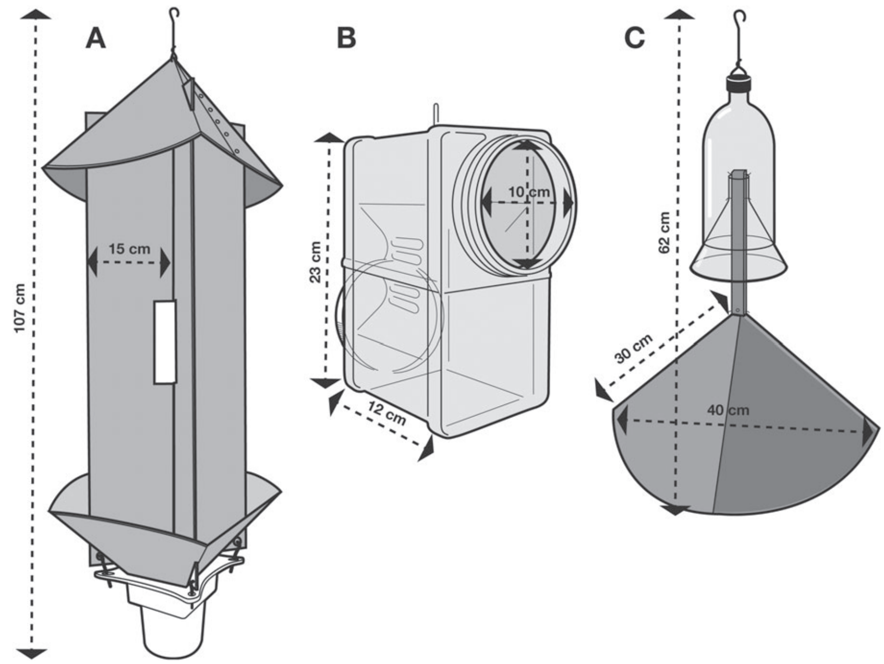

Figure 1 Three trap types used in the present study: (A) black and clear intercept panel trap; (B) newly-designed clear jar trap; and (C) newly-designed bell trap. Measurements of each trap are indicated in centimetres.

garage door. For illumination, 18 fluorescent bulbs were arranged transversely above the tunnel (40 W Gro-Lux wide-spectrum; Sylvania, Danvers, Massachusetts). These light bulbs provided illumination of 250 lux near the traps. Once again, continuous airflow was maintained at approximately 40–50 cm/s around the traps. In choice experiments, two traps were suspended side-by-side in the upwind end of the wind tunnel, approximately 1 m apart and 1.5 m above ground, presenting woodwasps with a choice.

In all experiments, woodwasps were transported in their cups within a cooler from the laboratory to the wind tunnel. Woodwasps were removed from the cooler at least 5 min before a flight, and were released at the centre of the downwind end of the wind tunnel. Woodwasps were either allowed to fly directly out of the cup or were carefully removed from the cup onto the hand of the researcher from which the woodwasp subsequently flew.

After a flight was initiated, a period of 3 min was allowed for a response, after which time the woodwasp was recorded as either captured in a trap or nonresponsive. Collection cups for traps did not contain ethylene glycol or other liquid, and so woodwasps were considered trapped if they ended up inside the collection cup. The number of wasps that landed on a trap without being captured was also recorded.

No-choice experiments

No-choice experiments were conducted in both 2011 and 2012. In 2011, we tested the three-component aggregation pheromone lure at two concentrations to determine which one should be used in field trapping studies, and they were tested using different trap designs in hopes of targeting male *S. noctilio*. Traps were baited with lures containing 0.1 or 1.0 mg of the aggregation pheromone [100 : 1 : 1 ratios of (*Z*)-3-decenol, (*Z*)-4-decenol and (*E*,*E*)-2,4-decadienal], prepared at the USDA APHIS PPQ Otis Quarantine Laboratory (Buzzards Bay, Maryland) (Cooperband *et al.*, 2012). The *Z*-3-decenol was synthesized in 2010 by Tappey Jones (Virginia Military Institute, Lexington, Virginia) and the unwanted *E* isomer was present at a 0.6% level. *Z*-4-decenol (97%) and *E*,*E*-2,4-decadienal (85%) were purchased from Sigma-Aldrich (St Louis, Missouri). The low concentration lures were used first to reduce the possibility of contamination of the wind tunnel. Pheromone lures were stored in sealed foil pouches at −20 °C before use. After opening a pouch, each lure was used for a maximum of 1 week.

The lures were tested in three traps: the widely used black intercept panel trap (IPM Technologies, Portland, Oregon) and two newly-designed prototype traps (named ‘clear jar’ and ‘bell’ traps) (Fig. 1). Each trap was placed individually in the upwind end of the wind tunnel in a ‘no-choice’ test, simply to quantify its capture rate. The traps were baited with either 0.1 or 1.0 mg of pheromone in rubber septa lures (details below). In 2012, the black intercept trap and the clear jar trap were used in ‘no-choice’ tests in the absence of any odours to determine whether they were, by themselves, differentially attractive to males and females.

In no-choice experiments, each woodwasp was tested once with each trap and no-choice comparisons were made using a nominal logistic regression chi-square test (JMP, version 10.0.0; SAS Institute Inc., Cary, North Carolina).

Choice experiments

In 2012, wasps were offered ‘choice tests’ between two traps. A black intercept panel trap was compared with a clear intercept

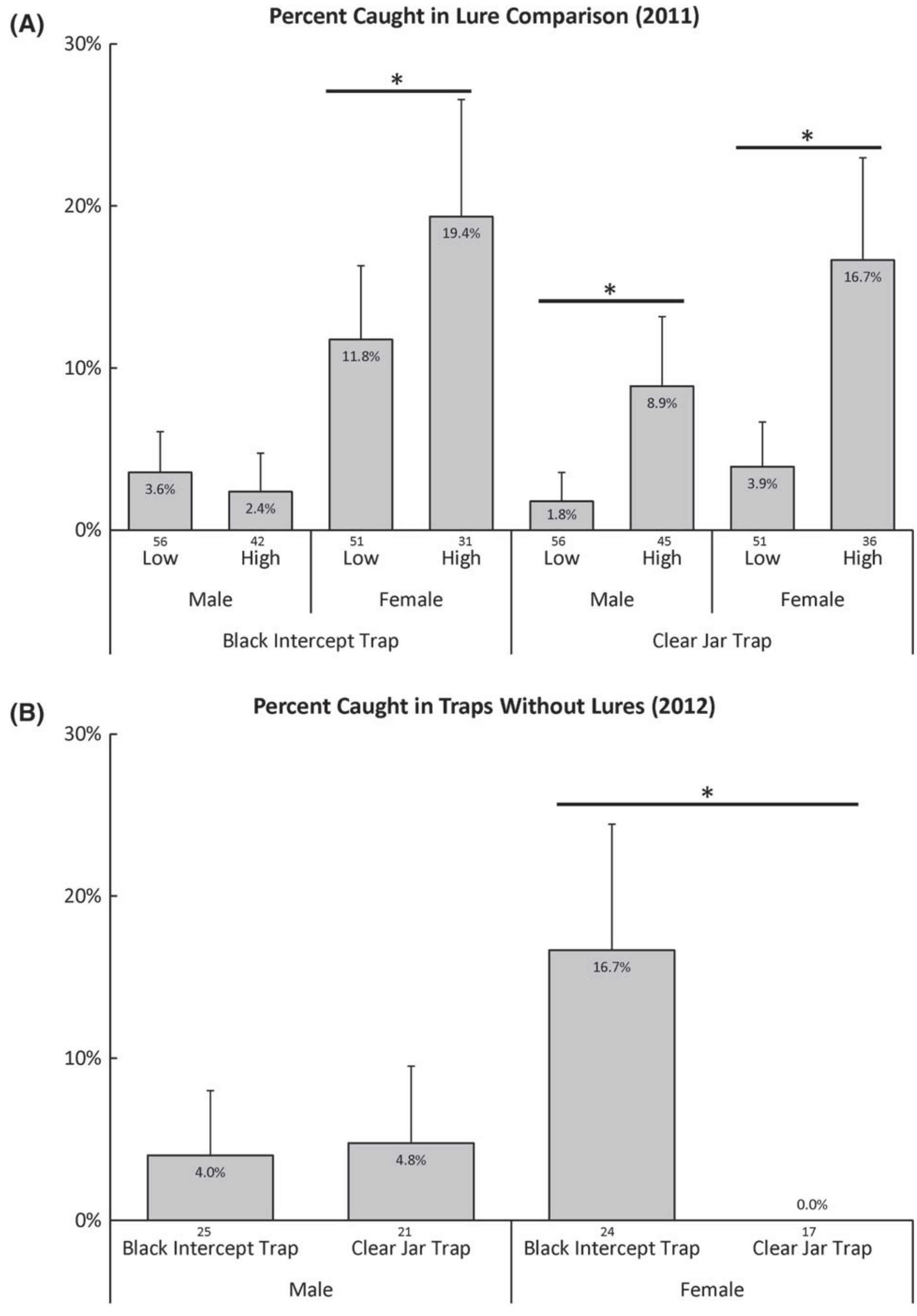

Figure 2 Percentages (± SE) of male and virgin female *Sirex noctilio* wasps that were released individually in the wind tunnel, flew upwind to a single trap and were captured by that trap. (A) In 2011, low (0.1 mg) and high (1.0 mg) dose pheromone lures (three-component blend) were compared in two types of traps. (B) In 2012, traps were compared without lures. Numbers below each bar represent the number of wasps released. Bars with asterisks represent significant differences between pairs tested using a nominal logistic chi-square test ($P = 0.05$).

panel trap to evaluate two equal trap designs of different appearances. These black and clear intercept traps were also baited with combinations of light and an eight-component blend kairomone [(+)-α-pinene (12.5%) (−)-α-pinene (12.5%), (−)-β-pinene (25.0%), (+)-3-carene (30.0%), (+)-camphene (5.0%), β-myrcene (10.0%), (+)-limonene (2.5%) and (−)-limonene (2.5%)] and tested in different comparisons.

Two traps were placed in the upwind end of the tunnel and baited with either nothing, a commercial *Sirex* kairomone lure containing an eight-component blend (Hurley *et al.*, 2014) (Alpha Scents, Inc., West Linn, Oregon), or an UV light (12-W fluorescent 'U'-shaped black light; BioQuip Products). All comparisons and numbers of insects tested are shown in Figs 2 and 3.

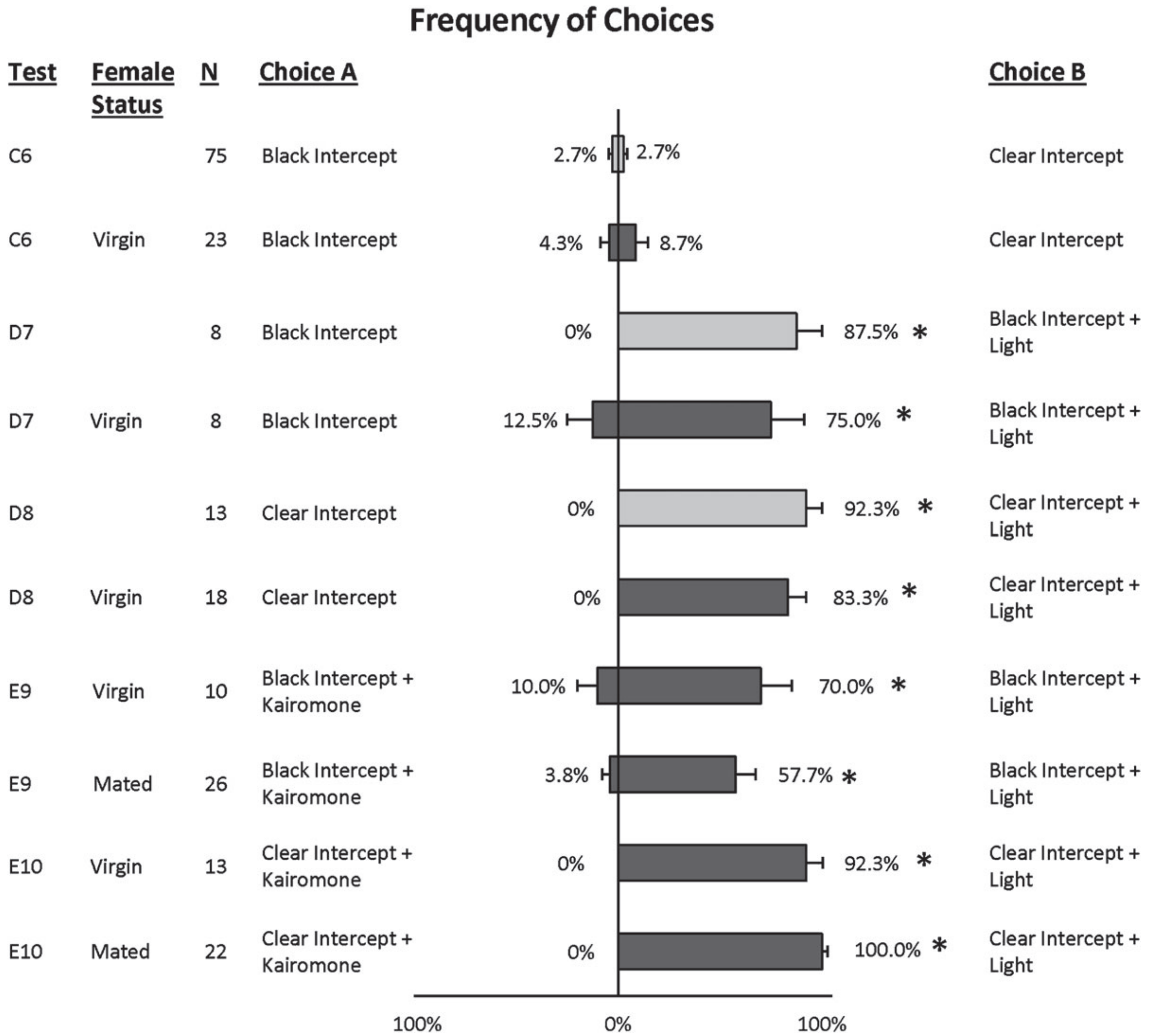

Figure 3 Frequency of choices by male (light bars) and female (dark bars) *Sirex noctilio* when released in the wind tunnel downwind of a pair of traps in 2012. Asterisks indicate a significant difference between the two traps (choice A and choice B) using a chi-square goodness of fit test ($P < 0.05$). Bars are labelled with the percentage of the released wasps that selected that choice; thus both choices combined represent the percentage of released wasps that responded by making a choice. Error bars represent SEs.

In choice experiments, woodwasps were tested twice because the positions of traps were interchanged to exclude any location bias. Choice experiments tested the null hypothesis that both choices were selected at the same frequency. Results were analyzed using the chi-square goodness of fit test. Differences were considered significant when the test statistic was $G \geq 3.841$ (d.f. $= 1$, $\alpha = 0.05$) (Sokal & Rohlf, 1995).

Results

No-choice experiments

Results from no-choice experiments in 2011 are depicted in Fig. 2(A). For the newly-designed clear jar trap, the higher-dose lure captured more males and females than the low-dose lure. The same pattern of catch increase with increased lure concentration was seen for females captured by the black intercept trap. However, few males were caught by the black intercept trap at either pheromone dose. The highest capture rates occurred with the 1-mg lure, which captured 19.4% of females in the black intercept trap and 8.9% of males in the newly-designed clear jar trap. For both pheromone concentrations, no *S. noctilio* of either sex were captured by the bell trap, and so it was excluded from further study. The results of the no-choice experiment in 2012 are depicted in Fig. 2(B). Both the unbaited black intercept trap and the unbaited clear jar trap caught similarly low numbers of males. However, the unbaited black intercept trap caught significantly more females (16.7%) than the unbaited clear jar trap, which did not catch any females.

Choice experiments

The results of the choice experiments are presented in Fig. 3. The capture rates of unbaited black intercept traps did not differ from the unbaited clear intercept traps for either males or virgin females. In all tests comparing a trap baited with UV light with a trap without light, there was a strong preference for the light-baited trap, even when the kairomone lure was the alternative. This was true regardless of whether the subjects were males, virgin females or mated females.

Discussion

The present study reports the capture rates of *S. noctilio* to traps in a large wind tunnel under semi-field conditions. When examining the new three-component pheromone blend, it was found to lure and trap up to 19.4% of females and up to 8.9% of males, although males and females responded differently to different trap designs. The black intercept trap was not effective at capturing males, although males could be captured by the newly-designed clear jar trap. Females could be captured by both traps when baited with 1 mg of pheromone blend. However, when both traps were tested without lures, females were only trapped by the black intercept trap, suggesting that there was a strong visual component to this trap. The present study confirmed the findings of Cooperband *et al.* (2012) showing that males avoided intercepting dark objects, even when they were attracted to them by pheromone. Not all traps work at a high rate of efficiency; indeed, a range of 5–20% efficiency exceeds the range of efficiency that can be expected by some of the best commercial mosquito traps available baited with CO_2 (Cooperband & Cardé, 2006b). However, intercept trap efficiency, at least for females, was as high as 100% when baited with UV light. Thus, trap efficiency may be improved in the field by the addition of UV light, rather than relying completely on olfactory attractants. The importance of visual cues in monitoring has recently been studied in the tropical root weevil *Diaprepes abbreviates* L., which showed a hierarchy between chemo- and phototaxis, and used visual cues in short-range host finding (Otalora-Luna *et al.*, 2013). A similar pattern of subordination of chemotaxis to phototaxis was shown in many Lepidoptera species (Shorey & Gaston, 1965; Balkenius *et al.*, 2006; Goyret *et al.*, 2007) and in the Colorado potato beetle *Leptinotarsa decemlineata* (Otalora-Luna & Dickens, 2011).

Although the black intercept trap by itself caught 16.7% of virgin females released, when placed side-by-side with a clear intercept trap, virgin females chose both traps at low frequencies, and did not show a preference between them, with 13% responding. Similarly, only 5.4% of males responded with no preference between black and clear intercept traps. However, when two identical intercept traps were placed side-by-side, and one was baited with an UV light, the response rate by males and females ranged from 61.5% to 100%, with most individuals choosing the trap baited with light, for both males and mated and virgin females. It is striking that males, which are normally averse to contacting black intercept traps even when baited with pheromone, were able to be captured at 87.5% when the traps were baited with UV light, and, when clear intercept traps were used, the male capture rate was 92.3%. Even when females were offered a choice between kairomone and UV light in two identical traps side-by-side, both virgin and mated females chose the traps baited with light, albeit mated females appeared to respond less strongly to the light-baited black intercept trap (57.7% captured) when the alternative was the black intercept trap baited with kairomone (only 3.8% captured).

Although the bell trap design did not catch any woodwasps in the present study, observations of the wasps approaching and contacting the traps showed that the bell trap provided a good landing surface for both sexes of *S. noctilio* but failed to capture the woodwasps because they did not crawl up into the collection container. Perhaps the application of an adhesive material to the surface of the bell trap could improve that design. Traps with sticky surfaces have successfully been used to monitor other forest pests, such as the emerald ash borer *Agrilus planipennis* Fairmaire (Crook *et al.*, 2012b; Domingue *et al.*, 2013a, b, and field studies using sticky traps for *S. noctilio* have had mixed success (K. Zylstra, personal communication).

Effective monitoring and early detection of the invasive woodwasp *S. noctilio* in the U.S.A. is challenging with the traps and lures currently available, especially in areas where wasp populations are low and host tree populations are patchy and irregular (Bashford, 2008; Dodds *et al.*, 2012; Jackson *et al.*, 2012). It has been reported that *S. noctilio* engage in positive phototaxis during their mating behaviour (Morgan & Stewart, 1966) and the use of visual cues has recently been shown to improve the trap design for other forest pests (Crook *et al.*, 2012b; Domingue *et al.*, 2013a,b). Although unbaited traps did not strongly attract woodwasps, the addition of UV light significantly increased the success of *S. noctilio* capture. The use of light as an attractant in traps has long been employed for detecting a variety of flying insects such as wood-borers, moths and mosquitoes (Barnes *et al.*, 1965; Ritchie & Kline, 1995; Meierrose *et al.*, 1996; Bashford, 2008). It is known that intercept panel traps baited with kairomone are successful at capturing *S. noctilio* females (Bashford, 2008; Hurley *et al.*, 2014) and these wind tunnel studies strongly suggest that the addition of UV light to those traps may enhance trap capture for both sexes.

Acknowledgements

We thank Sirex-wrangler Stefan Long for help with finding and cutting down *Sirex*-infested trees and organizing the collection of *S. noctilio* from emergence barrels. I. Caetano mated woodwasps with assistance from E. Morris and S. Kroll. A. Anderson and S. Andrews helped with wind tunnel trials. A. Hartness assisted in the original construction of the wind tunnel. R. Kepler and J. Liebherr assisted with reassembly and later modification of the wind tunnel. We thank Kitty Gifford and Tim Youngs from Mad Men Fridays Design for their assistance with the illustrations. We also thank the anonymous reviewers for their thoughtful comments. Funding for the present study was provided through a cooperative agreement with USDA APHIS. Mention of a commercial product does not constitute an endorsement or recommendation for its use by the USDA.

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Accepted 3 June 2014
First published online 4 August 2014