



Phenology and flight periodicity of *Sirex noctilio* (Hymenoptera: Siricidae) in central New York, U.S.A.

Scott W. Myers*, Kelley E. Zylstra*, Joseph A. Francese*, Daniel M. Borchert† and Sian M. Bailey*

*Center for Plant Health Science and Technology, USDA-APHIS, Buzzards Bay, MA, 02542, U.S.A. and †Center for Plant Health Science and Technology, USDA-APHIS, Raleigh, NC, 27606, U.S.A.

- Abstract**
- 1 Field and laboratory studies were performed to determine the phenology of flight activity and the thermal requirements for adult emergence of *Sirex noctilio*.
 - 2 Degree-day (DD) accumulation from egg to adult was measured in bolts of *Pinus sylvestris* infested with eggs from laboratory-reared adults. Adult emergence was similarly monitored in bolts from trees that were naturally infested in the field by wild populations of *S. noctilio* reared at constant temperature.
 - 3 Laboratory-infested bolts produced mostly males, whereas field-collected material produced a 2.7 : 1 male-biased sex ratio. Mean DDs to emergence was 1477.0 ± 13.4 (males) in laboratory-infested bolts, as well as 1455.2 ± 11.2 (males) and 1577.8 ± 19.5 (females) in field-collected material.
 - 4 Field-trapping studies were conducted to compare flight activity with rearing data. Trap captures showed first flight activity and peak catch occurred at 709 and 1145 DDs. The resulting degree-day model predicts early flight activity in early to mid-April for pine stands in southeastern U.S.A., early to mid-May in the Mid-Atlantic region, and late June to early July in the northeast.

Keywords Degree-days, European wood wasp, forest pests, invasive species.

Introduction

When exotic insects are introduced and become established in a new environment, survey tools are useful to determine the extent of establishment and to monitor their dispersal and colonization of new areas. This is particularly important for large scale survey efforts that can be costly in terms of resources and time invested. Insects are poikilothermic and, as such, degree-day (DD) models based on heat unit accumulation, within upper and lower developmental thresholds, have proven reliable for predicting the development of many insects that we are interested in monitoring. Lifecycle events of numerous economical important pests are monitored across broad geographical scales using a variety of DD-based models (Johnson *et al.*, 1983; Maiorano, 2012). Typically, they are used to time pest control measures when a particular life stage is targeted, although DD models are also useful to optimize efforts in monitoring population spread and abundance. Degree-day based phenology models of flight activity can help focus trapping efforts to reduce labour in trap collections, minimize

the time traps are in the field and make the most of pheromones and other attractants when they are employed.

The recent establishment of *Sirex noctilio* in North America provided an opportunity to study and evaluate flight activity of this insect in a new environment where it has been infesting native and non-native trees. *Sirex noctilio* was first observed in central New York from a funnel-trap catch in 2004 (Hoebeker *et al.*, 2005) and has subsequently been detected in Connecticut, Ohio, Michigan, Pennsylvania and Vermont, as well as Ontario and Quebec, Canada (Dodds & de Groot, 2012; Zylstra & Mastro, 2012). *Sirex noctilio* has a broad host range within the *Pinus* genus, with many hosts in its native and introduced range (Spradbery & Kirk, 1978). The heaviest infestations in central New York are found in stands of the European native *Pinus sylvestris* (Scots pine) (Eager *et al.*, 2011; Zylstra & Mastro, 2012). These are typically dense and unmanaged stands susceptible to drought stress and insect attack, which may contribute to their appeal to *S. noctilio* females. North American natives *Pinus strobus* (white pine), *Pinus resinosa* (red pine) and *Pinus banksiana* (Jack pine) are also confirmed hosts of *S. noctilio* (Dodds *et al.*, 2010) and have been found infested throughout the range of *S. noctilio* in the U.S.A. and Canada (Dodds & de Groot, 2012).

Correspondence: Scott W. Myers. Tel.: +1 508 563 0959; fax: +1 508 564 4398; e-mail: scott.w.myers@aphis.usda.gov

It is likely that *S. noctilio* will continue to expand its range in North America through natural migration because much of the eastern U.S.A. contains suitable host material and predictive models suggest that it is likely to survive in these areas (Carnegie *et al.*, 2006). As *S. noctilio* range expands southward, it poses a potential threat to pine resources in the southeastern U.S.A. where many economically important pine species are grown in managed stands (Gaby, 1985). Optimized survey and trapping information is needed to detect newly-developing populations. A better understanding of the phenology of *Sirex* adult emergence and flight activity will facilitate the development of optimal data collection methodology.

The present study aimed to determine the timing of flight activity in the eastern U.S.A. through trapping efforts and to compare these results with emergence data collected under controlled conditions in the laboratory. The overall goal was to use a DD model to predict larval development and adult emergence in Scots pine. This information could aid survey and detection efforts monitoring the movement of *S. noctilio* populations in the U.S.A.

Materials and methods

Infestation of P. sylvestris bolts

To evaluate the developmental time for *S. noctilio* from egg to adult, bolts of *P. sylvestris* were infested using adult *S. noctilio* females reared from pine bolts that were cut from winter-harvested trees. Upon emergence, adult females were collected and placed in screen-topped, clear plastic 2.0-L containers with three males for 12–24 h. After a female was observed mating with one of the males, she was removed and placed in one of two plexiglass cages (2.0 × 0.65 × 0.55 m) containing six *P. sylvestris* bolts (diameter 1 m, length 7–10 cm) oriented vertically. Bolts were cut from two *P. sylvestris* trees that were located well outside the current known range of *S. noctilio* in North America. The ends of each bolt were coated with AnchorSeal® petroleum wax sealant (UC Coatings Corporation, Buffalo, New York) to reduce drying within 24 h of felling, and the bolts were allowed to dry for six additional days before the first mated *S. noctilio* females were introduced to the cages. A total of 13 and eight females were introduced to the first and second cages, respectively. Females typically lived 7–10 days in the chamber and were observed drilling into the bolts. After bolts were infested, they were held at ambient laboratory temperatures (22.0 ± 1.0 °C) until adults emerged and were collected. HOBO® data loggers (model U12-015; Onset Computer Corp., Bourne, Massachusetts) were used to record temperature during the developmental period. Dates of adult emergence and the sex of each individual were recorded.

Rearing of S. noctilio in field-girdled P. sylvestris trees

Thirty field sites were established from 2008 to 2010 (10/year) in forested stands of *P. sylvestris* in central New York to collect *S. noctilio* infested trees (Fig. 1). Field sites were located by crews visually searching for resin symptoms indicative of *S. noctilio* infestation (Ryan *et al.*, 2013) in areas where it

was previously known to occur. Particular effort was made to find field sites across as broad a geographical area as possible. The majority of sites were set up as a single group of three trap trees at each forest stand location. However, several locations provided sufficient room to establish multiple sites; these were spaced a minimum of 100 m apart. Sites where no *S. noctilio* adults were collected were excluded from the experiment because no trees were harvested. To attract adult females and improve the level of infestation, *P. sylvestris* trees were chemically girdled in the last week of May or the first week of June using the herbicide Banvel® (BASF Corp., Germany) [480 g/L 3,6-dichloro-o-anisic acid (dicamba)] just before the adult flight period. This has been shown to facilitate oviposition by *S. noctilio* (Neumann *et al.*, 1982; Wermelinger & Thomsen, 2012). Four trees at each site were girdled in accordance with the methods described by Zylstra *et al.* (2010). Holes of approximately 1.9 cm in diameter and 10 cm in depth were drilled every 10 cm around the base of each tree. A 5-mL solution of a 1 : 1 mixture of formulated product and water was injected into each hole using a 25-mL plastic syringe. The girdled trees were felled from October to December each year and cut into bolts measuring approximately 70 cm, starting from approximately chest height on the tree bole to just beneath the crown. Bolts with fresh resinosis were selected for rearing adults. The ends of each bolt were coated with AnchorSeal®. Bolts were transported to the USDA Otis Laboratory insect containment facility (Buzzards Bay, Massachusetts) where they were arranged horizontally in plastic barrels (diameter 50 cm, length 75 cm) with window screen tops, with three to eight bolts in each barrel. Temperature was maintained at 23.0 ± 1.0 °C to allow adults to emerge from the logs. Barrels were checked daily during the work week and occasionally on weekends. The emergence date and sex of each individual was recorded. A subset of 361 males and 146 females collected from bolts in 2009 were weighed to compare emergence time with body mass. An additional subset of 50 bolts were dissected 60 days after the last adult emerged using an electric powered hydraulic wood splitter to collect any life stages of *S. noctilio* remaining in the wood. The bolt dissections were used to evaluate the success of larval development to adult under these conditions and to determine what proportion of *S. noctilio* larvae may require a longer period of development. The number and life stage of *S. noctilio* found in the wood were recorded.

Field trap captures

To compare adult emergence time in the laboratory with flight periods in the field, trap catch data were collected from sites across 11 counties in New York state from 2007 to 2010. Field sites included the 21 locations that were used to collect *S. noctilio* infested trees in the previous section (2008–2010). At each of these locations, HOBO Pendant® data loggers (model: 8K - UA-002-08) were used to collect daily temperatures at 1-h intervals. An additional 46 locations across central New York from related projects on *S. noctilio* were also included (Fig. 1). Data from the 2007 sites were previously reported by Zylstra *et al.* (2010). Trap trees were chemically girdled using herbicide as above, or with Garlon 3A™ [trimethylamine salt

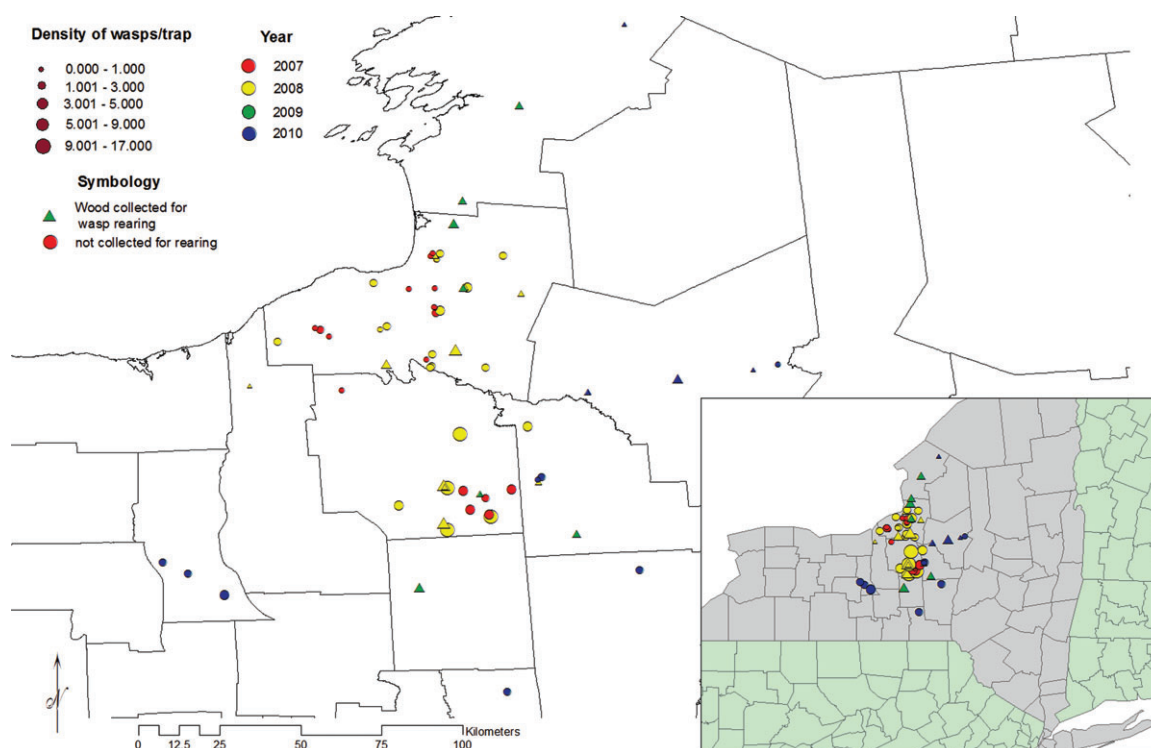


Figure 1 Location of *Sirex noctilio* trapping and wood tree harvest sites in central New York during 2007–2010.

of triclopyr (3,5,6-trichloro-2-pyridinyloxyacetic acid); 360 g/L; Dow Agrosciences LLC, Indianapolis, Indiana] using the same procedure, or mechanically girdled to attract females. Mechanically girdled trees were created by cutting through the phloem and cambium and into the sapwood at approximately 1.5 m with a chainsaw. The cut was continued around the tree for the entire circumference. A second, identical cut was made 15 cm below this cut, and all bark material was removed from between the two cuts. Lindgren funnel traps without lures (12-funnel; Contech Inc., Canada; Synergy Semiochemicals, Canada) were hung at 6.1 m from *P. resinosa* and *P. sylvestris* trees in areas assumed to be infested. Traps cups were filled to a depth of 2.5 cm with undiluted propylene glycol (Peak RV and Marine Antifreeze, Old World Industries, Northbrook, Illinois). Data from 2008 include a trap type study (three sites) where cross-vane and panel traps were used in addition to Lindgren funnel traps. Cross-vane traps (33 × 120 cm) were produced from black corrugated plastic (Coroplast Inc, Dallas, Texas). Black corrugated plastic squares (33 × 33 cm) were attached to the top and bottom of each trap. Panel traps were cut (100 × 50 m) from plastic hardware cloth (1.3-cm mesh). Both cross-vane and panel traps were coated with Tanglefoot Insect Trap Coating (brushable formulation; Contech Inc., Grand Rapids, Michigan) to catch adult *S. noctilio*. Trap collections were made weekly from late June to September.

Statistical analysis

The single sine method for DD calculations (Baskerville & Emin, 1969) was used to calculate DD for adult emergence in

the laboratory and flight in the field (from 1 January) using the base developmental threshold of 6.8 °C from Madden (1981). An upper development temperature of 35.0 °C was used based on Madden (1981), which indicated a decline in *S. noctilio* development and survival above 33.5 °C. Minimum and maximum daily temperatures were derived from data loggers when they were associated with trapping sites. When the trapping locations did not have data loggers, daily temperature data were used from the nearest NOAA, National Climatic Data Center land-based data station (NCDC, 2013). A *t*-test was used to compare mean DD for adult emergence between males and females in the laboratory, and between laboratory-reared and field-collected adult females. Probit regression models were used to fit the cumulative proportion emergence data from laboratory-reared and field-collected *S. noctilio* using SAS, version 9.3 (SAS Institute, 2011). First flight and peak flight predictions were based on 5% and 50% emergence estimates, respectively, from the probit model. Data are reported as the mean ± SE, as well as median emergence estimates from probit regression models with 95% confidence intervals.

Using the DD modelling function in the North Carolina State University-APHIS Plant Pest Forecasting (NAPPPFAST) system (Borchert & Magarey, 2007), DD models were created using 6.8 °C as the base developmental temperature and the model was initiated to start accumulations on 1 January of each year. The NAPPPFAST system produced GeoTIFF raster maps with 10 km² resolution that use multiple years of data (10, 20 or 30) to display the frequency with which an event occurs during the time period of interest. The geotiff rasters were manipulated and combined for display using ARCGIS ARCFINFO, version 10

(ESRI, Inc., Redlands, California). Frequency maps were set to display the area and the time for DD accumulation to initial and peak emergence, respectively. The map was reclassified into a single class for all occurrences more frequent than 3 years. Map generation and reclassification for subsequent time periods were performed to illustrate where and when initial and peak emergence of *S. noctilio* would occur in the eastern U.S.A.

Results

Infestation of *P. sylvestris* bolts using laboratory-mated *S. noctilio* females produced highly-skewed sex ratios. A total of 142 adult males and two females emerged from the two groups of six 1-m length bolts. The first adult emerged after 71 days and the last was collected at 115 days. Mean time and DD to emergence was 91.2 ± 0.83 and 1477.0 ± 13.4 days, respectively.

A total of 741 males and 272 females (2.72:1, M:F) adult *S. noctilio* were reared from 162 *P. sylvestris* bolts collected in the field over 3 years (2008–2010) (Fig. 2). Adult males emerged as early as 43 days after they were introduced to 23 °C temperature and the latest to emerge was a female at 190 days. Despite different starting points (egg versus larva), mean DD to emergence was similar to that of the laboratory-infested bolts, with no significant difference found between males from each group (d.f. = 619, $t = -0.22$, $P = 0.829$). A significant difference in mean DD to emergence was, however, observed between male (1455.2 ± 11.2) and female (1577.8 ± 19.5) adults reared in the laboratory from field-collected bolts (d.f. = 1011, $t = -5.58$, $P < 0.0001$). Median emergence time as estimated from probit regression models was 1445 (1380, 1516) and 1559 (1478, 1638) for males and females, respectively. No significant year effect on DD to emergence was observed for either sex (d.f. = 2, $F = 0.08$, $P = 0.93$). Dissection of the sub-sample of 50 *P. sylvestris* bolts collected in the fall of 2009 that produced 527 live adults yielded an additional 102 dead adults, 51 dead larvae and six live late-instars inside the wood. Mean weights of adult males (38.2 ± 1.5 mg; $n = 465$) and females (94.3 ± 5.1 mg; $n = 178$) reared from bolts collected in 2009 and 2010 field seasons were significantly different (d.f. = 658, $t = -14.96$, $P < 0.001$), although no relationship between body mass and time to emergence was found for either sex.

A total of 1067 females were collected in traps over the 4 years and emergence patterns were similar (Fig. 3). The earliest emergence was observed at approximately 700 DD, whereas mean DD catch was 1158.3 ± 7.3 for the combined data from all 4 years. Linear regression of probit-transformed data provided a good fit for both cumulative proportions of trapped females in the field, as well as cumulative emergence of adults in the laboratory (Fig. 4). The number of *S. noctilio* females captured in traps in the field varied considerably from year to year, and the variability may have been the result of the number of traps included, the overall level of infestation across field sites and the effectiveness in timing tree girdling to lure adult females to the traps.

Regression models of probit-transformed cumulative trap catch data predicted 5% trap catch (early emergence) occurring

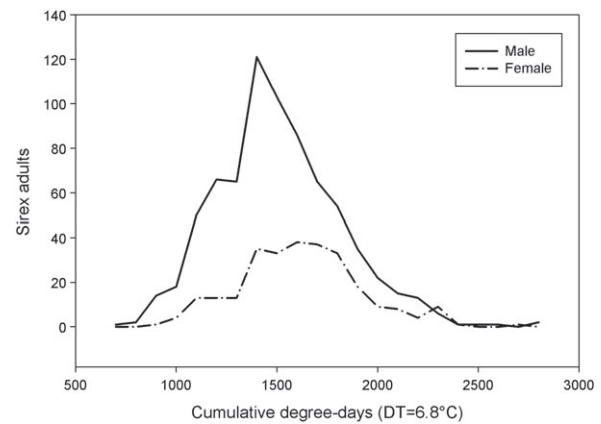


Figure 2 Emergence of *Sirex noctilio* adults from winter-harvested *Pinus sylvestris* collected in New York from 2008 to 2010 reared in the laboratory at 23.0 ± 1.0 °C. DT, developmental threshold.

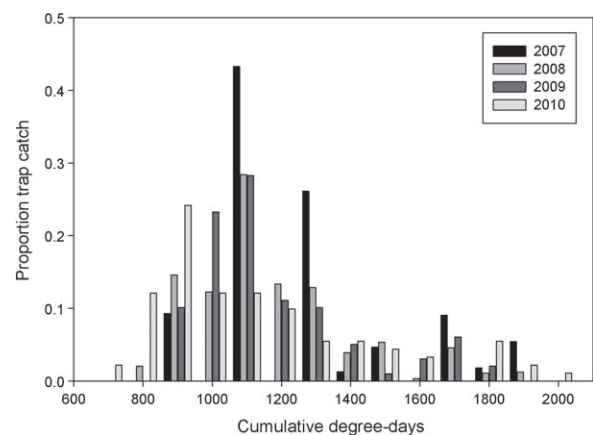


Figure 3 Proportional distribution of *Sirex noctilio* adult females captured in traps from 4 years of field surveys in central New York. One thousand and sixty-seven total adults captured, all female (2007: $n = 387$; 2008: $n = 507$; 2009: $n = 100$; 2010: $n = 73$).

at 709 DD and 50% catch at 1145 DD. This coincides with late June to early July in northern Pennsylvania and central New York, where *S. noctilio* is currently known to occur. If this relationship holds true in warmer parts of the U.S.A., some of the pine growing regions from eastern Texas to northern Florida and southern portions of Georgia and South Carolina would experience first emergence of adults as early as mid-April and peak flight activity during the first half of May (Fig. 5).

Discussion

On comparing rates of development under constant temperature in the laboratory, we found that adults emerged from winter field-collected material at a similar DD to that in the laboratory-infested bolts. We know from previous dissections of field-collected host trees that *S. noctilio* are mid- to late-instar larvae during the winter months. This result suggests that *S. noctilio* larvae in field-collected material are in winter diapause, and that there is a delay in resuming development

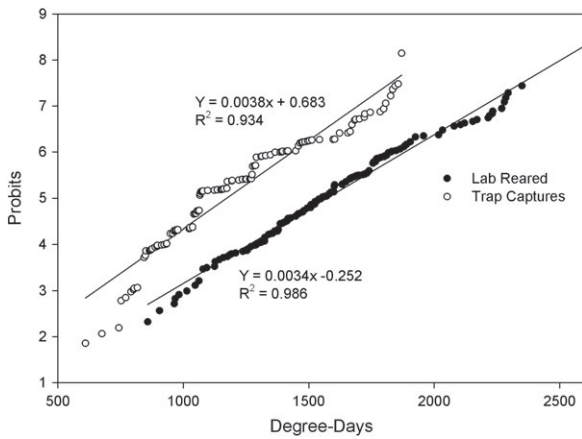


Figure 4 Cumulative trap catch of *Sirex noctilio* females in the field (2007–2010; $n = 1067$) and laboratory-reared adults from field-collected bolts (2008–2010; $n = 1012$).

after they were brought indoors and acclimated to 23 °C. Larvae developing in laboratory-infested bolts do not require a diapause and thus are able to develop to adulthood without delay.

Similarly, in the field, cumulative mean DD trap catch for females was significantly less than DD accumulation to emergence for field-collected material that was brought into the laboratory and held at constant temperature. Mean emergence was 409 DD higher in field-collected material reared in the laboratory compared with trap captures (Fig. 4). This suggests that over-wintering larvae in the field are presumably able to break diapause and resume development as field temperatures become favourable without the delay in development that is experienced by larvae in winter-collected bolts.

Both our field and laboratory results showed peak emergence to occur considerably sooner than the 2500 DD reported by Madden (1981). The difference could be attributable to differences in development in the different tree species used and the overall suitability of the bolts for growth of *A. areolatum*. The range of the adult emergence period was much greater (124 days) in the field-collected material than it was for the laboratory-infested material (44 days). Although some of this difference reflects the larger sample size of laboratory material, variation in oviposition dates of females in the field, as well as differences in the sub-cortical temperatures experienced by individuals depending on tree location and solar exposure, would also contribute to a broader emergence period. Morgan (1968) suggested that percentage cloud cover and atmospheric

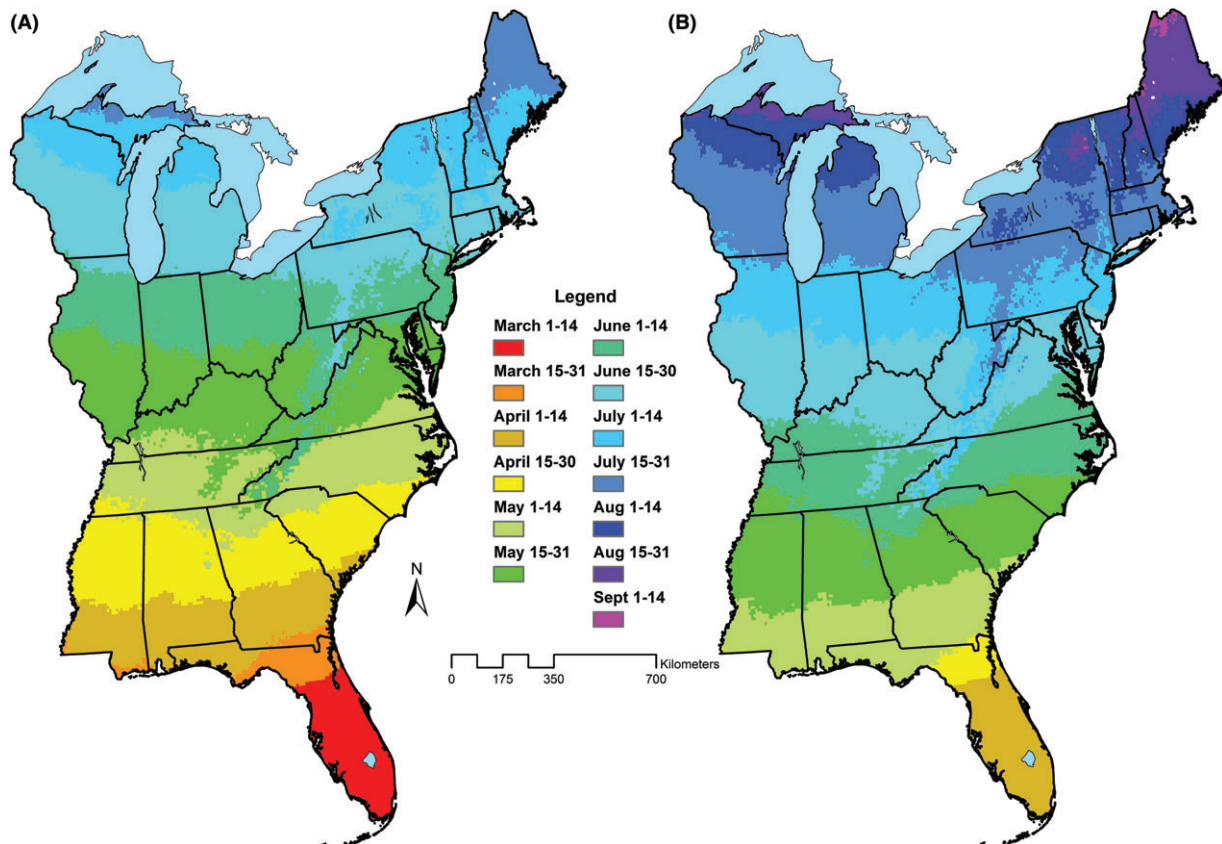


Figure 5 Degree-day model predictions of first emergence (A) (700 DD) and peak adult flight (B) (1145 DD) for *Sirex noctilio* in the eastern U.S.A. Degree-day calculations were based on a developmental threshold of 6.8 °C and upper threshold of 35 °C. Probit regression of cumulative adult female trap captures in central New York from 2007 to 2010 was used to estimate early and peak emergence periods using 5% and 50% cumulative emergence estimates, respectively.

pressure changes influence *S. noctilio* emergence rates and that delayed emergence can affect adult size. However, we found no correlation between adult body mass and time of development, which indicates other factors likely account for the variability that we saw within the same bolt.

Bolt dissections also revealed a larger than expected number of dead adults (approximately 15%) remaining in the wood. Similar data collected from *P. sylvestris* bolts that were held vertically in individual emergence barrels with little or no contact with the sides of the barrels found 586 adults and 32 dead larvae, although no live larvae or dead adults remaining in 48 logs that were dissected > 60 days from the last adult to emerge (S. W. Myers, unpublished data). These results suggest that adults may have trouble emerging from logs when they are blocked by other logs or the sides of barrels when barrels contain multiple logs and/or the barrels are held horizontally, as was the case in the present study.

The strongly male-biased sex ratio resulting from laboratory infestations indicates that, although the females were observed to copulate with males before they were introduced to the pine bolts, they may not have successfully mated and, as such, unfertilized females would have only been able to produce male offspring. Alternatively, females may have been reluctant to oviposit fertilized eggs in an artificial environment or consider cut bolts as a poor host and consequently deposited predominantly male eggs, similar to other xylophagous hymenoptera that have been shown to alter sex ratios in response to host plant quality (Craig *et al.*, 1992; Mopper & Whitham, 1992). In addition, the majority of the adult males that emerged were very small, which could have been a result of poor fungal colonization by the symbiotic *Amylostereum* fungus. Madden and Coutts (1979) attributed variation in adult size to differences in fungal growth patterns and development within and among different host trees, with larger individuals arising from areas where fungal growth was highest. The bolts used for this experiment were freshly-harvested from healthy trees and may not have provided an optimum growth environment for the fungus. Madden (1981) was successful in using laboratory-mated females to infest *P. radiata* bolts in the laboratory but did not report the sex ratio of emerged adults. Similarly, Rawlings (1953) was also able to rear *S. noctilio* in cut *P. radiata* bolts, although they did report a 10:1 male-biased sex ratio. Other researchers in the U.S.A. have reported similar results of skewed sex emergence when infesting cut pine bolts. Dinkins *et al.* (2011) released both sexes in large cages to allow females to oviposit into bolts of several species of pines and produced only male progeny.

Dissections of field-collected material after adult emergence found 0.8% (six of 680 individuals) of larvae alive that would have likely had an extended diapause into a second year. This is consistent with the findings of Spradbery and Kirk (1978) who found 1.6% of adults emerging after 2 years and 0.04% emerging after 3 years in a variety of conifers collected throughout Europe. Ryan *et al.* (2012) found 4.1% adult emergence the second year from bolts of *P. banksiana*, *P. sylvestris* and *P. resinosa* stored in emergence containers. Other reports suggest that as many as 25% of *S. noctilio* larvae extend diapause and emerge as adults 2 or 3 years post oviposition in Australia (Taylor, 1981) and Patagonia (Corley & Villacide,

2012), although there is little supporting data available in the literature.

Cutting trees into bolts and holding them for emergence at constant light and temperature likely discouraged extended diapause in the overwintering larvae by providing favourable conditions for them to resume development. Although the bolt ends were sealed, they were still more prone to drying than standing trees in the field. It is possible that *S. noctilio* prefers the upper portions of trees for oviposition and larval development because the wood is drier than the lower portions, and moisture reduction may promote pupation (Morgan & Stewart, 1966; Morgan, 1968). However, Ryan *et al.* (2013) found the majority of *S. noctilio* induced resinosis in the mid-bole section of *P. sylvestris* trees in Ontario, Canada. An additional consideration is the effect of chemical girdling, which resulted in rapid death of the tree. This may have contributed to a faster rate of larval development and/or a reduction in the portion of larvae extending diapause. This aspect of larval development warrants further attention because delayed adult emergence may increase the probability of spread to new areas. If viable larvae can remain in cut logs or other wood products for multiple years, they are more likely to be transported to new areas through human-mediated movement.

Certainly, there are a number of environmental factors that may contribute to differences in emergence patterns of *S. noctilio* inhabiting different host trees on different continents. Although our results show consistent annual patterns of emergence, development times and DD relationships may change as *S. noctilio* moves southward and encounters a warmer climate and new host conifers. Based on DD alone, the warmer temperatures in the southeastern U.S.A. suggest the possibility of multiple generations per year; however, multivoltine populations have not been noted in other parts of the world with similarly warm climates (e.g. South Africa, Australia, southern Brazil). The degree-day relationship provided here provides a starting point to guide survey efforts currently ongoing in many eastern states. The importance of more accurate timing is especially important with *S. noctilio* because current trapping methods are inefficient and may not readily detect low level populations in areas where it is newly established.

Acknowledgements

The authors wish to thank Mike Crawford and Susan Carlton for their many hours in the field working on the trapping portion of this project. We also thank Miriam Cooperband, Peggy Elder, Colin Geisenhoffer, Helen Hull-Sanders, Patrick Pendergast, Jamie Savje and Rebecca Timson for their contributions and support. Ken Bloem, Robyn Rose and Kimberly Wallin critiqued earlier versions of this manuscript and provided many helpful comments. Funding for this project was provided by the USDA-APHIS *Sirex noctilio* programme.

References

- Baskerville, G.L. & Emin, P. (1969) Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology*, **50**, 514–517.

- Borchert, D.M. & Magarey, R.D. (2007) *A Guide to the Use of NAPFFAST* [WWW document]. URL www.nappfast.org [accessed on 13 November 2013].
- Carnegie, A.J., Matsuki, M., Haugen, D.A. *et al.* (2006) Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. *Annals of Forest Science*, **63**, 119–128.
- Corley, J.C. & Villacide, J.M. (2012) Population dynamics of *Sirex noctilio*: influence of diapauses, spatial aggregation and flight potential on outbreaks and spread. *The Sirex Woodwasp: Expanding Frontiers* (ed. by B. Slippers, M. J. Wingfield and P. de Groot), pp. 51–64. Springer, The Netherlands.
- Craig, T.P., Price, P.W. & Itami, J.K. (1992) Facultative sex ratio shifts by a herbivorous insect in to variation in host plant quality. *Oecologia*, **92**, 153–161.
- Dinkins, J. (2011) *Sirex noctilio* host choice and no-choice bioassays: woodwasp preferences for southeastern US pines. M. S. Thesis, pp. 27–57. University of Georgia, Athens, Georgia.
- Dodds, K.J. & de Groot P. (2012) *Sirex*, surveys and management: challenges of having *Sirex noctilio* in North America. *The Sirex Woodwasp: Expanding Frontiers* (ed. by B. Slippers, M. J. Wingfield and P. de Groot), pp. 265–286. Springer, The Netherlands.
- Dodds, K.J., de Groot, P. & Orwig, D.A. (2010) The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario. *Canadian Journal of Forest Research*, **40**, 212–223.
- Eager, P.T., Allen, D.C., Frair, J.L. & Fierke, M.K. (2011) Within-tree distributions of the *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) – parasitoid complex and development of an optimal sampling scheme. *Environmental Entomology*, **40**, 1266–1275.
- Gaby, L.I. (1985) *The Southern Pines: Loblolly Pine (Pinus taeda L.), Long Leaf Pine (Pinus palustris Mill.), Shortleaf Pine (Pinus echinata Mill.), Slash Pine (Pinus elliotti Engelm.)*. United States Department of Agriculture, Forest Service Publication, FS-256 Washington, D.C.
- Gandhi, K.J.K., Dinkins, J.E., Riggins, J.J. *et al.* (2011) Colonization preferences of the European woodwasp, *Sirex noctilio*, on southeastern pine species. Proceedings of the Interagency Research Forum on Exotic Insects, pp. 73–74, 11–14 January 2011. Annapolis, Maryland.
- Hoebeke, E.R., Haugen, D.A. & Haack, R.A. (2005) *Sirex noctilio*: discovery of a Palearctic siricid woodwasp in New York. *Newsletter of the Michigan Entomological Society*, **50**, 24–25.
- Johnson, P.C., Mason, D.P., Radke, S.L. & Tracewski, K.T. (1983) Gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), egg eclosion: degree-day accumulation. *Environmental Entomology*, **12**, 929–932.
- Madden, J.L. (1981) Egg and larval development in the woodwasp *Sirex noctilio* F. *Australian Journal of Zoology*, **29**, 493–506.
- Madden, J.L. & Coutts, M.P. (1979) The role of fungi in the biology and ecology of woodwasps (Hymenoptera: Siricidae). *Insect – Fungus Symbiosis: Nutrition, Mutualism and Commensalism* (ed. by L. R. Batra), pp. 165–174. Wiley & Sons, New York, New York.
- Maiorano, A. (2012) A physiologically based approach for degree-day calculation in pest phenology models: the case of the European corn borer (*Ostrinia nubilalis* Hbn.) in Northern Italy. *International Journal of Biometeorology*, **56**, 653–659.
- Mopper, S. & Whitham, T.G. (1992) The plant stress paradox: effects on pinyon sawfly sex ratios and fecundity. *Ecology*, **73**, 515–525.
- Morgan, F.D. (1968) Bionomics of Siricidae. *Annual Review of Entomology*, **13**, 239–256.
- Morgan, F.D. & Stewart, N.C. (1966) The biology of the woodwasp *Sirex noctilio* (F.) in New Zealand. *Transactions of the Royal Society of New Zealand*, **7**, 195–204.
- Neumann, F.G., Harris, J.A., Kassaby, F.Y. & Minko, G. (1982) An improved technique for early detection and control of the *Sirex* wood wasp in radiata pine plantations. *Australian Forestry*, **45**, 117–124.
- [NCDC] National Climatic Data Center (2013) *Land Based Data Center*. Satellite and Information Service, National Environmental Satellite, Data and Information Service [WWW document]. URL <http://www.ncdc.noaa.gov/oa/land.html> [accessed 5 July 2013].
- Rawlings, G.B. (1953) Rearing of *Sirex noctilio* and its parasite *Ibalia leucospoides*. *New Zealand Forest Research Notes*, **1**, 20–34.
- Ryan, K., de Groot, P. & Smith, S.M. (2012) Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*. *Agricultural and Forest Entomology*, **14**, 187–195.
- Ryan, K., de Groot, P., Smith, S.M. & Turgeon, J.J. (2013) Seasonal occurrence and spatial distribution of resinosis, a symptom of *Sirex noctilio* (Hymenoptera: Siricidae) injury, on boles of *Pinus sylvestris* (Pinaceae). *Canadian Entomologist*, **145**, 117–122.
- SAS Institute (2011) *SAS 9.3 Users Guide*. SAS Institute Inc., Cary, North Carolina.
- Spradbery, J.P. & Kirk, A.A. (1978) Aspects of the ecology of siricid woodwasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research*, **68**, 341–359.
- Taylor, K.L. (1981). The *Sirex* woodwasp: ecology and control of an introduced forest insect. *The Ecology of Pests: Some Australian Case Histories* (ed. by R. L. Kitching and R. E. Jones), pp. 231–248. CSIRO, Australia.
- Wermelinger, B. & Thomsen, I.M. (2012) The woodwasp *Sirex noctilio* and its associated fungus *Amylostereum areolatum* in Europe. *The Sirex Woodwasp: Expanding Frontiers* (ed. by B. Slippers, M. J. Wingfield and P. de Groot), pp. 65–80. Springer, The Netherlands.
- Zylstra, K.E., Dodds, K.J., Francese, J.A. & Mastro, V. (2010) *Sirex noctilio* in North America: the effect of stem-injection timing on the attractiveness and suitability of trap trees. *Agricultural and Forest Entomology*, **12**, 243–250.
- Zylstra, K.E. & Mastro, V. (2012) Common mortality factors of woodwasp larvae in three northeastern U.S. host species. *Journal of Insect Science*, **12**, 83.

Accepted 28 October 2013

First published online 26 December 2013