Seasonal Phenology of Sirex nigricornis (Hymenoptera: Siricidae) in Arkansas with Implications for Management of Sirex noctilio

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Seasonal phenology of *Sirex nigricornis* (Hymenoptera: Siricidae) in Arkansas with implications for management of *Sirex noctilio*

Jessica A. Hartshorn, Danielle M. Fisher, Larry D. Galligan, and Fred M. Stephen

Abstract

The southeastern United States contains a multi-billion dollar pine timber industry that could be affected significantly by the establishment and spread and of *Sirex noctilio* F. (Hymenoptera: Siricidae), the non-native wood wasp that was discovered recently in the northeastern United States. Several factors, including the timing of native wood wasp (*S. nigricornis* F.) emergence and flight, may influence the success of *S. noctilio*. Understanding the seasonal phenology of the native wood wasp will allow us to make better predictions regarding the potential ecological impacts by *S. noctilio* on Arkansas pine forests. Native *S. nigricornis* females were collected across 3 geographic regions of Arkansas from 2009 to 2013 using intercept panel traps baited with *Sirex* lure (70/30-α/β-pinene blend) and ethanol. A Gompertz 3-parameter model was fitted to each year of trapping as well as a final dataset containing all trapping seasons. Emergence rates and inflection points of the models did not differ among geographic regions within any year but did change significantly among years. In regions where both wood wasps occur, native wood wasps emerge in the fall and attack dead pines, whereas *S. noctilio* emerges much earlier and attacks live, standing trees. We expect these patterns to remain very similar upon the spread of *S. noctilio* into the Southeast. Therefore, we do not expect these 2 species to utilize the same hosts or emerge at the same time in Arkansas, which makes native species displacement unlikely. Additional studies examining the effects of predators, parasitoids, and competitors on *Sirex* population dynamics would greatly enhance these predictions.

Key Words: flight period; climate; *Sirex* lure

Resumen

El sudeste de los Estados Unidos tiene una industria de madera de pino de millones de dólares que podría ser afectada de manera significativa por el establecimiento y expansión de *Sirex noctilio* F. (Hymenoptera: Siricidae), la avispa no nativa de la madera, que fue descubierta recientemente en el noreste de los Estados Unidos. Varios factores, incluyendo el tiempo de la emergenica y el vuelo de la avispa nativa de la madera (*S. nigricornis* F.), pueden influir en el éxito de *S. noctilio*. Al entender la fenología estacional de la avispa nativa de la madera nos permitirá hacer mejores predicciones sobre el posible impacto ecológico de *S. noctilio* en los bosques de pino de Arkansas. Se recolectaron hembras nativas de *S. nigricornis* en 3 regiones geográficas de Arkansas desde 2009 hasta 2013 utilizando paneles trampa de intercepción cebadas con un señuelo para *Sirex* (mezcla de 70/30-α/β-pineno) y etanol. Un modelo Gompertz de 3 parámetros fue encajado por cada año de la captura, así como un último conjunto de datos que tenia todas las estaciones de trampeo. Las tasas de emergencia y los puntos de inflexión de los modelos no difieren entre regiones geográficas dentro de un año, pero varió significativamente entre años. En las regiones donde se encuentran ambas avispas de la madera, las avispas nativas de la madera emergen en el otoño y atacan pinos muertos mientras que *S. noctilio* emergen mucho antes y atacan a los árboles parados y vivos. Esperamos que estos patrones se mantengan muy similar a la expansión de *S. noctilio* en el sureste. Por lo tanto, no esperamos que estas 2 especies utilizan los mismos hospederos o emerjan al mismo tiempo en Arkansas, lo que hace poco probable el desplazamiento de la especie nativa. Estudios adicionalies que examinen los efectos de los depredadores, parasitoides y competidores sobre la dinámica poblacional de *Sirex* mejoraría en gran medida estas predicciones.

Palabras Clave: período de vuelo; clima; señuelo para *Sirex*

Sirex nigricornis F. (Hymenoptera: Siricidae) is found throughout the eastern United States and Canada and is the most commonly encountered pine-inhabiting wood wasp native to Arkansas (Schiff et al. 2006). Adults are univoltine, emerging from early Oct through the end of Dec, and their regional abundance varies greatly (Barnes 2012; Hartshorn 2012; Keeler 2012; Lynn-Miller 2012). In their respective native ranges, *Sirex* wood wasps rarely attack healthy vigorous trees and often develop in trees that previously were stressed or injured (Hall 1968; Coyle et al. 2012).

In 2004, an invasive European wood wasp, *Sirex noctilio* F. (Hymenoptera: Siricidae), was detected in upstate New York (Hoebeke et al. 2005). This species has been introduced accidentally into several countries in the Southern Hemisphere, where pines are not native, and frequently has caused widespread tree mortality by tunneling through the xylem and interfering with nutrient translocation (Rawlings & Wilson 1949; Ciesla 2003). This was in part because of poor silvicultural and management practices, but also because the complex of insects, fungi, and nematodes that commonly interact with *Sirex* species in

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their respective native ranges was absent at the time of introduction. Dinkins (2011) reported that *S. noctilio* will oviposit and complete development in pines native to the southeastern U.S. This creates concern that *S. noctilio* will establish in, and become a pest of, pine timber stands in Arkansas and surrounding states, especially in areas with poor silvicultural practices (Chase et al. 2014). Potential threats resulting from the establishment of the non-native species in the Southeast include ecological and economic damage to both commercial and unmanaged pine forests, and the possible displacement of native wood wasps (Gandhi & Herms 2010; Ryan et al. 2012). However, we lack information on native wood wasp ecology that will enable us to better predict interactions among these species.

Some studies (e.g., Zylstra et al. 2010) have described seasonal flight patterns of *S. noctilio* but have not examined yearly variation in these patterns. Herein, we analyzed standardized trap captures of *S. nigricornis* among regions and over several years, and compared the emergence patterns in relation to possible interactions between the 2 wood wasp species. Our objectives were to 1) use *S. nigricornis* trap catch data, collected from 2009 to 2013 across 3 geographic regions of Arkansas to describe and model the onset, duration, and patterns of adult female flight, and 2) qualitatively compare this information to existing phenological studies of *S. noctilio* to evaluate the potential for interactions among the native and invasive wood wasps, as well as other pine-inhabiting insects.

Materials and Methods

SITE SELECTION

Three geographic locations in Arkansas were chosen to represent forests of varying topography, climate, and stand composition (Ozark National Forest, Ouachita National Forest, and Gulf Coastal Plains). Sites were on both public and private land, and areas with obvious damage (e.g., from tornadoes, ice storms) were included to ensure capture of wood wasps as we anticipated that these sites comprised favorable habitat. We identified stands that contained mostly shortleaf (*Pinus echinata* Mill.) and/or loblolly pine (*P. taeda* L.) (Pinales: Pinaceae). Matching these criteria meant that regions in which we trapped changed from year to year (Fig. 1). Each site in 2009 (7 sites), 2010 (14 sites), and 2011 (10 sites) contained 3 traps. Twelve sites in 2012 and 8 sites in 2013 each contained 2 traps.

Descriptions of Ozark and Ouachita National Forests follow the eco-subregion descriptions by McNab & Avers (1994). Diameter at breast height (DBH) reported was collected once at each site during *Sirex* trapping. Sites in the Ozark and Ouachita National Forests were dominated by oak, hickory, and pine species. In the Ozarks, elevation ranged from 200 to 793 m. Pine DBH averaged 30 cm with a range of 19 to 40 cm. In the Ouachitas, elevation ranged from 100 to 793 m. Pine DBH in the Ouachita
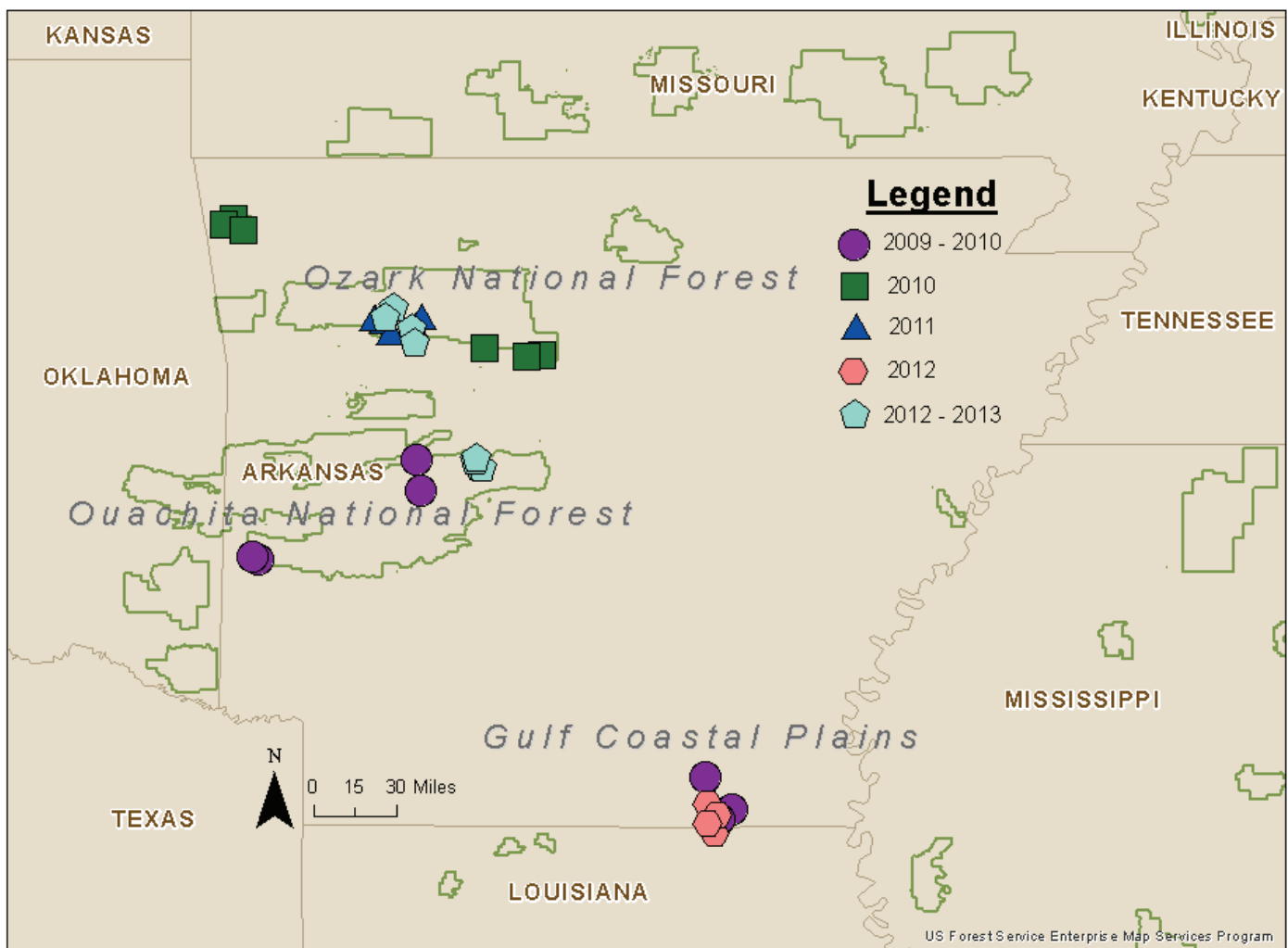

Fig. 1. Map showing all trapping sites from 2009 to 2013 in Arkansas, USA. Legend indicates which sites were trapped during which years.

sites averaged 25 cm with a range of 22 to 31 cm. The Gulf Coastal Plains sites were characterized as a southern floodplain consisting of mainly oak–hickory forests with intensively managed loblolly pine stands intermixed. Elevation was much lower (0 to 91 m) relative to both the Ozarks and Ouachitas. DBH of pines in the Gulf Coastal Plains sites averaged 21 cm with a range of 17 to 26 cm (Keeler 2012; Lynn-Miller 2012).

FIELD TRAPPING

Intercept™ panel traps (APTIV Inc., Portland, Oregon, USA) baited with *Sirex* lure (70% α-pinene, 30% β-pinene; 2.0 g/d release rate) and ultra-high release (UHR) ethanol (0.70 g/d release rate) (Synergy Semiochemicals Corp., Burnaby, British Columbia, Canada) were used for all years. In 2009, traps were erected in mid-Oct and adult flight was missed partially. Traps in 2010 to 2013 were therefore erected in late-Sep to detect the first emergence of females. Traps in all years were collected until at least 2 collections contained no *Sirex* (late Dec). Lures were replaced halfway through each trapping season (mid-Nov). Traps were hung from a 19 mm diameter (¾ inch) steel electrical conduit that was bent using a conduit bender to form an inverted L-shape. A hole was drilled in the top bent portion of the bar from which traps were hung with wire. For all years except 2011, traps terminated in a collection cup that contained propylene glycol (Super Tech RV and Marine®) for the capture and preservation of insects. To avoid damage from black bears, poles were raised using additional conduit until collection cups were approximately 2.5 m above the ground (Barnes 2012; Coyle et al. 2012).

In 2011 only, a second collection method was used in the Ozark National Forest to collect live insects for additional laboratory experiments. Because for that year only the Ozarks were represented, regional differences could not be tested. The trap type and lures were as above, APTIV Intercept™ panel traps baited with *Sirex* lure and UHR ethanol, with the addition of ipsenol, ipsdienol, and lanierone (Synergy Semiochemicals Corp., Burnaby, British Columbia, Canada) to increase the diversity of wood-boring insects captured. Instead of a collection cup filled with propylene glycol, a 125 L (33 gallon) Rubbermaid® trash can was attached to the base of each panel trap to create a modified live-trapping system (Lynn-Miller 2012). All traps were placed approximately 50 m from each other. All trap contents were collected every 7 to 14 d and held in cold storage until processing. Wood wasp females were counted, used for laboratory rearing studies, and stored in vials containing 95% ethanol after natural death.

STATISTICAL ANALYSES

JMP Pro 11 (SAS Institute, Cary, North Carolina, USA) was used for all statistical analyses. Variation in numbers of traps used at sites and

among years existed, and high variation in individual trap catch densities even within individual sites was common. Additionally, successive trap collection periods were not always the same number of days. Therefore, counts of trapped *S. nigricornis* were standardized by converting to relative proportions (i.e., each collection day wood wasp count was divided by the total number of wood wasps captured in each trap, at each site, for each year). Relative proportions were then summed to produce cumulative proportion distributions that measured rate of capture irrespective of absolute density and were not biased by variations in time intervals between successive collection periods (Stephen & Dahlsten 1976). We summed these proportions over the entire trapping season to obtain a standardized scale of wood wasp emergence from zero to one over time (expressed as Julian date). When no significant differences were seen among geographic regions, cumulative proportions were calculated for each year, combining all regions.

Several model types were first analyzed for all years of trapping. A Gompertz 3-parameter model provided the best fit to each year of data:

$$Cumulative\ Proportion = a \times e^{-e^{[-b(Julian\ Date-c)]}},$$

where a = asymptote, b = capture rate, and c = inflection point. For each year, a Gompertz 3-parameter model was fitted to cumulative proportions of wood wasps and grouped by regions. A test for parallelism was then performed to detect significant differences in emergence patterns among regions. Data collected in 2011 were not grouped by region because only the Ozark National Forest was represented. For all other years, regions were never significantly different from each other so all regions were combined and a new Gompertz 3-parameter model was fitted to the entire dataset for each year (Table 1). Finally, all datasets were combined and a Gompertz 3-parameter model was fitted to these data and grouped by year. A test for parallelism was performed to test for significant differences among years. All significance reported is based on α = 0.05. Per trap means were not included due to high variation within sites. The inflection point is the Julian date at which the concavity of the model changes and capture rate begins to slow. Because the measured variable was cumulative proportion, the asymptote for each model was always close to one. Capture rate can be interpreted as the proportion of wood wasps captured per day during each respective trapping season and cannot be extrapolated to the entire calendar year or to other trapping seasons of different lengths.

Results

From 3 Nov to 9 Dec 2009, 180 wood wasps were collected in 21 total traps. Even with the setback of late trap placement, geographic

Table 1. Parameter estimates of Gompertz 3-parameter models for each individual year of *Sirex nigricornis* trapping from 2009 to 2013 in Arkansas, USA.

Year	Asymptote (± SE)	Capture rate (± SE)	Inflection point (± SE)	RMSE[a]	*R*-square
2009	1.0097 (0.0432)	0.1498 (0.0197)	312.2838 (0.7054)	0.0794	0.9568
2010	1.0843 (0.0325)	0.0629 (0.0041)	302.3386 (0.7879)	0.0437	0.9875
2011	0.9616 (0.0253)	0.1069 (0.0092)	300.2624 (0.5583)	0.0719	0.9634
2012	1.7614 (0.1835)	0.0263 (0.0024)	332.3699 (4.3324)	0.0491	0.9794
2013	0.9982 (0.0175)	0.1077 (0.0070)	317.9811 (0.4230)	0.0624	0.9767

Significance is based on α = 0.05.
[a]RMSE, root mean square error, is a measure of the differences between the value projected by the model and the values actually observed.

regions did not significantly differ from each other (F = 0.276; df = 2; P = 0.7629). The final Gompertz 3-parameter model predicted a capture rate of 0.1498 ± 0.0197 (SE) with an inflection point at 312 ± 0.7054 (SE) d, which corresponds to 8 Nov (Fig. 2; R^2 = 0.9568).

From 24 Sep until 6 Dec 2010, 186 *Sirex* females were trapped in 42 total traps. No significant difference was detected among regions (F = 2.201; df = 4; P = 0.0852). The final model predicted a capture rate of 0.0629 ± 0.0041, which was much slower compared with 2009 (Fig. 3; R^2 = 0.9875). This could be an artifact of erecting traps earlier in 2010 compared with the previous year. The inflection point was approximately 10 d earlier than the previous year (JD = 302 ± 0.7879 d; 29 Oct), which could also be related to earlier trap placement.

From 12 Oct until 8 Dec 2011, 141 female wood wasps were captured in 30 traps in the Ozark National Forest. The model predicted a capture rate of 0.1069 ± 0.0092 and an inflection point of 300 ± 0.5583 d, corresponding to 27 Oct (Fig. 4; R^2 = 0.9634).

A surge of adult wood wasps was captured in 2012 with 357 being collected in 24 traps between 8 Oct and 20 Dec 2012. Even with a much larger emergence of wood wasps compared with the previous years, geographic regions were not significantly different (F = 0.930; df = 4; P = 0.4512). The capture rate for 2012 was the slowest of all trapping seasons at 0.0263 ± 0.0024. The inflection point was at the latest date compared with other years at 332 ± 4.3324 d, or approx. 27 Nov (Fig. 5; R^2 = 0.9794).

In 2013, total trap catch numbers dropped to 95 wood wasps collected from 16 traps over the longest period of emergence from 3 Oct to 31 Dec. Geographic regions were again not significantly different from one another (F = 0.492; df = 2; P = 0.6133). The capture rate increased to 0.1077 ± 0.0070 compared with the previous year. The inflection point was earlier, Julian date 317 ± 0.4230 d, or 13 Nov (Fig. 6; R^2 = 0.9767).

COMBINED YEARS

In total, 959 wood wasps were collected from 2009 to 2013. Emergence began in early Oct and ceased in mid- to late Dec, which agrees with other reports of *Sirex* emergence in the Southeast (Haavik et al. 2013). A test of parallelism found significant differences among years (F = 48.621; df = 8; P < 0.0001), and a final model (Fig. 7; Table 2) including all datasets fit less well than individual years' models (R^2 = 0.8582). Inflection points for each year within the final model were very similar to their respective individual models, except for 2012, which had an
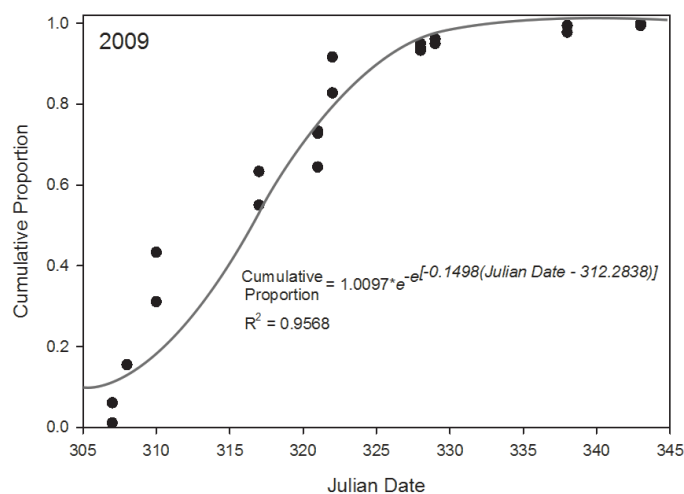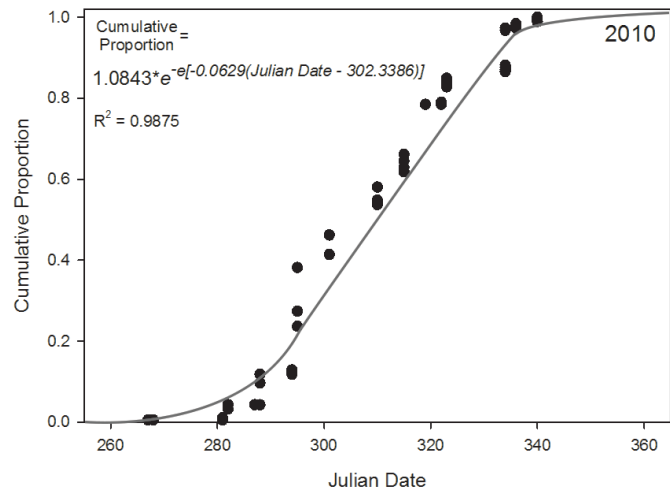

Fig. 3. Gompertz 3-parameter model fit to cumulative proportion of wood wasps captured in Arkansas, USA, from 24 Sep to 6 Dec 2010.

inflection point 16 d earlier than the individual model for that year. The inflection point for the overall model, encompassing 5 trapping seasons, was 310 d, or 6 Nov.

With the exception of 1 *Sirex* female captured on 24 Sep 2010, captures began the 1st week of Oct and continued into Dec for each year. Captures lasted longest in 2013, continuing to 31 Dec.

Discussion

Although raw numbers of *Sirex* females cannot be compared directly due to variability among sites, trap number, and collection frequency, it is worth noting that 2009–2011 saw comparable trap captures of wood wasps, whereas 2012 saw a surge of wood wasp emergence, and 2013 saw a large drop off in numbers of wood wasps captured. It is unlikely that this decrease in numbers of *Sirex* captured resulted from a "trap-out" phenomenon. The *Sirex* lure does not contain sex or aggregation pheromones, but rather host volatiles, and is not considered any more effective at attracting females than a cut or damaged pine tree. The mechanisms behind the large emergence of 2012 are unknown but the previous, abnormally warm winter is suspected to have played a role. Temperatures in Arkansas over the winter of 2011–
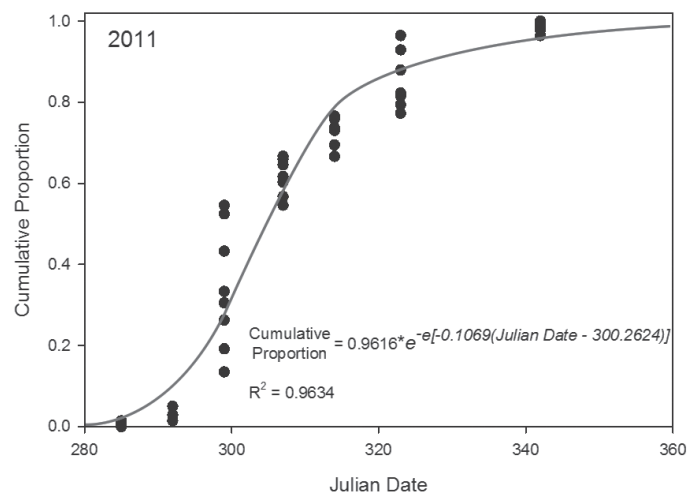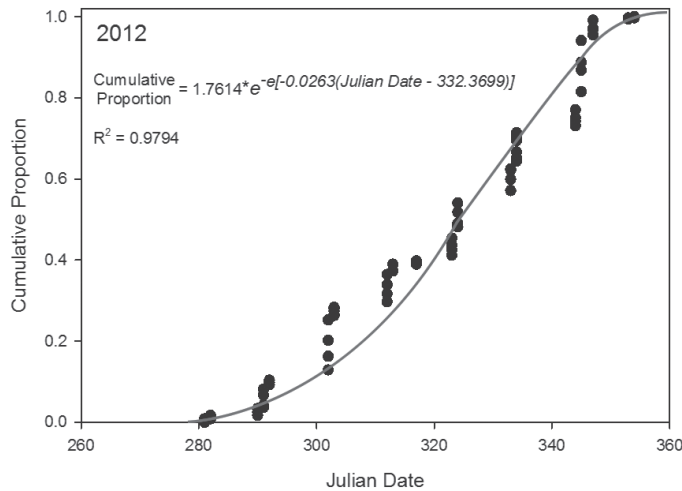

Fig. 2. Gompertz 3-parameter model fit to cumulative proportion of wood wasps captured in Arkansas, USA, from 3 Nov to 9 Dec 2009.

Fig. 4. Gompertz 3-parameter model fit to cumulative proportion of wood wasps captured in Arkansas, USA, from 12 Oct to 8 Dec 2011.
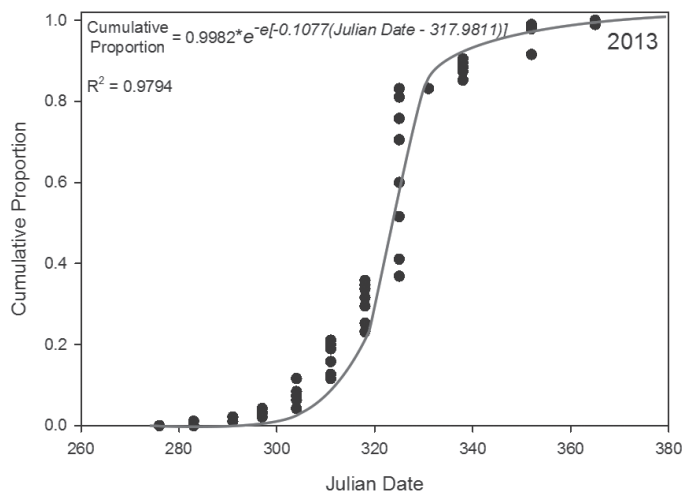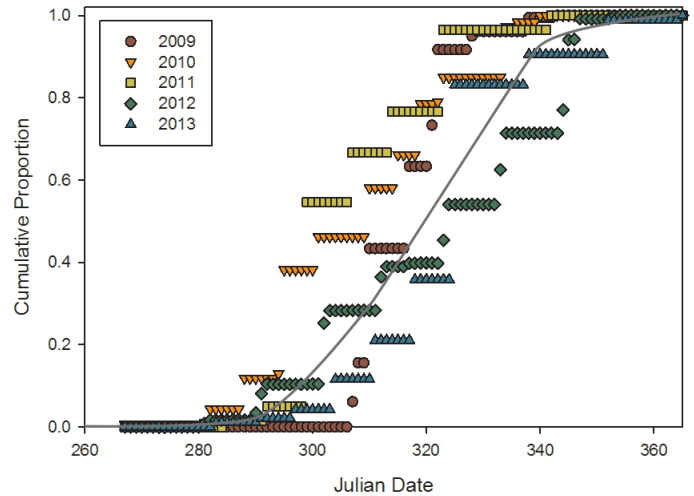
Fig. 5. Gompertz 3-parameter model fit to cumulative proportion of wood wasps captured in Arkansas, USA, from 8 Oct to 20 Dec 2012.

Fig. 7. Gompertz 3-parameter model fit to all 5 *Sirex nigricornis* trapping seasons; a = 1.0628, b = 0.0575, c = 309.5517; R^2 = 0.8582. The inflection point for the overall model, encompassing 5 trapping seasons, was 310 d, or 6 Nov. Legend indicates which data points correspond to which year.

2012 rarely dipped below the developmental minimum of *S. noctilio* (Madden 1981), presumably similar to the developmental minimum of *S. nigricornis*, and reached above 21 °C several times. The following winter (2012–2013) contained several severe winter weather events and was followed by a relatively cool summer (National Oceanic and Atmospheric Administration 2014), which may have caused increased mortality resulting in the apparent population decline that occurred during the 2013 trapping season.

Inflection points differed by more than a month among the 5 trapping seasons. The inflection point for the overall model, encompassing 5 trapping seasons, was 310 d, or 6 Nov. Capture rates also changed significantly during that time. The slowest rate of capture was seen in 2012 at 0.0263 and the highest was in 2009 at 0.1498. However, 2012 also had the largest number of wood wasps captured, and 2009 was the shortest trapping season due to problems obtaining permits and establishing sites. These issues resulted in traps not being erected until late Oct. Therefore, the start of wood wasp emergence (capture) cannot be described accurately for 2009. These stark differences in capture rates could be an artifact of these issues. Even with large changes in emergence from year to year, the overall pattern of captured fly-

ing females beginning in early Oct, peaking in Nov, and waning in Dec, stayed consistent.

Lantschner et al. (2014) described the spread of *S. noctilio* being closely tied to latitudinal temperature increases. They suggested that wood wasp activity will increase and emergence will begin earlier in warmer climates, such as those in the Southeast. With respect to native wood wasps, we found that, even with numbers of captured adults more than doubling in the 2012 trapping season, presumably due to high winter temperatures, emergence did not begin earlier than in other years. However, if this trend of higher winter temperatures continued over several years, we might expect to see earlier emergence of natives if they follow the same early patterns as *S. noctilio* does in consistently warmer temperatures. Zylstra et al. (2010) showed that 79% of captured *S. noctilio* were collected in New York, USA, by the beginning of Aug and all *S. noctilio* had been captured by the end of Sep. Haavik et al. (2013) found *S. noctilio* emerging from Jul through Sep in Ontario, Canada, and their findings are consistent with additional studies (e.g., Myers et al. 2014), which predict future *S. noctilio* emergence in the Southeast occurring as early as mid-Apr. These patterns indicate that *S. nigricornis* and *S. noctilio* will not overlap in seasonal flight patterns, even in the warmer climate of the Southeast. However, this does not suggest that the southeastern U.S. will escape establishment by *S. noctilio*.

Additionally, by the time of predicted *S. noctilio* emergence in the Southeast, several other pine-inhabiting insects are already present, and some of these can significantly impact the successful development

Fig. 6. Gompertz 3-parameter model fit to cumulative proportion of wood wasps captured in Arkansas, USA, from 3 Oct to 31 Dec 2013.

Table 2. Parameter estimates for Gompertz 3-parameter model of all combined years of *Sirex nigricornis* trapping from 2009 to 2013 in Arkansas, USA.

Parameter	Year	Estimate	Standard error
Asymptote	—	1.0449	0.0208
Capture rate	—	0.0719	0.0037
Inflection point	2009	310.2977	0.9576
Inflection point	2010	302.0973	0.8740
Inflection point	2011	301.1619	0.7077
Inflection point	2012	316.7971	0.7254
Inflection point	2013	317.4866	0.6850

Years are significant ($P < 0.0001$) based on α = 0.05.

of *S. noctilio.* Ryan et al. (2012) provided evidence suggesting increased mortality of *S. noctilio* in pine trees when other pine-inhabiting beetles are present. Many of these beetles, namely *Pissodes nemorensis* Germar, *Ips grandicollis* Eichhoff, various ambrosia beetles (Coleoptera: Curculionidae), and *Monochamus* spp. (Coleoptera: Cerambycidae), commonly are encountered in Arkansas and may serve as competitors that slow establishment of *S. noctilio*.

In addition to pine-inhabiting beetles, there are several parasitoids that are native to the southeastern U.S. (Kirk 1974), and commonly are collected in traps or from rearing bins along with *S. nigricornis* adults. Some of these parasitoids (e.g., *Ibalia leucospoides* [Hochenwarth]; Hymenoptera: Ibaliidae) have been introduced as biological control agents of *S. noctilio* in the Southern Hemisphere and have been largely successful (Carnegie et al. 2005). However, Yousuf et al. (2014) described issues with using these native species for biological control in North America due to the fungal interactions between bark beetle fungi (*Ophiostoma* spp.; Ophiostomatales: Ophiostomataceae) and the symbiotic fungus of *Sirex* spp. (*Amylostereum* spp.; Russulales: Amylostereaceae). It is expected that the parasitic nematode *Deladenus* (Tylenchida: Neotylenchidae) would also have an effect on the establishment of *S. noctilio* in the Southeast. It parasitizes the eggs, mycangia, and hemocoel of female wood wasps, leaving wasps unable to lay viable eggs (Keeler 2012; Kroll et al. 2013; Zieman 2013). All of these previously mentioned species could inhabit the same resource as *S. noctilio*, and these multi-trophic interactions should be examined closely as part of any comprehensive management recommendations.

In conclusion, although rates of capture and inflection points may change significantly from year to year, the onset and duration of native wood wasp flight do not differ significantly. We find native wood wasps in the Southeast emerging much later than *S. noctilio* in other parts of North America and believe this is an indication that the 2 species will not overlap during flight or development within host trees. Although they may overwinter in the same hosts, their developmental stages during this time are likely to be different. We also note the presence of common beetle species and natural enemies that may hinder *S. noctilio* survival, emergence, and establishment. Investigation into this interspecific competition among native and non-native wood wasps is currently underway.

Acknowledgments

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