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Predicting *Sirex noctilio* and *S. nigricornis* emergence using degree days

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Abstract

The study of temporal interactions between native insects and alien invaders can be facilitated by the ability to forecast adult emergence. We used field-collected adult emergence data of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a woodwasp native of Eurasia that has recently invaded northeastern North America, and *Sirex nigricornis* Fabricius, a woodwasp native to North America, to develop and test cumulative degree-day (CDD) models. Five data sets were collected each in Ontario, Canada (*S. noctilio*) and Louisiana, USA (*S. nigricornis*) over 4 years; three data sets were used to develop models and two were used to test them. Males and females of each species were modelled separately. After testing several potential temperatures, chosen thresholds for CDD were 0 °C lower threshold and 25 °C upper threshold for both *Sirex* spp. We used a three-parameter Gompertz growth function to model *Sirex* spp. emergence against CDD. Models predicted 10% emergence of *S. noctilio* in Ontario after 1 239 and 1 280 CDD, for males (start date = 1 April; $R^2 = 0.91$) and females (start date = 1 April; $R^2 = 0.86$), respectively. Models predicted 10% emergence of *S. nigricornis* in Louisiana after 3 980 and 5 016 CDD, for males (start date = 1 May; $R^2 = 0.83$) and females (start date = 1 March; $R^2 = 0.73$), respectively. Cumulative degree-day models predicted 10 and 90% emergence of woodwasp populations with less error (1–13%) than they did 50% emergence (5–27%). For both *Sirex* spp., male emergence began a few days before and concluded at about the same time as that of females. In southern Ontario, models predict that *S. noctilio* adults will be in flight between 1 015 and 2 430 CDD (1 April start date for CDD; from early-July until mid-September). In Louisiana, models predict that *S. nigricornis* adults will be in flight between 3 854 and 4 700 CDD (1 May start date for CDD; from early-October until late-November).

Introduction

Insects are poikilothermic, and their development is directly related to temperature. Heat unit accumulation calculated by degree days has long been used to predict emergence of adult insects (Pruess, 1983; Higley et al., 1986). The degree-day approach uses minimum and maximum daily air temperatures, along with inputs of lower and upper temperature thresholds for development, and computes the number of heat units accumulated above the lower (when no upper threshold is specified) or between these two thresholds on a daily basis (Pruess, 1983; Higley et al., 1986). Temperature thresholds and optimum temperatures for insect development can be determined experimentally in the laboratory (e.g., Régnière & Turgeon, 1989; Keena & Moore, 2010). Temperature thresholds can also be determined by trial and error from iterations of models developed from field-collected emergence data (e.g., Akers & Nielsen, 1984; Smith et al., 2004). We used the latter approach (i.e., field-collected data) to develop degree-day models that predicted emergence of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) adults in southern Ontario, Canada, and emergence of *Sirex nigricornis* Fabricius adults in Louisiana, USA.

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Both woodwasp species attack *Pinus* spp. (Pinaceae) and are not economically important pests within their native ranges (Hall, 1968; Kirk, 1974). In North America, *S. noctilio* is a newly introduced (2004) invasive species from Europe (Hoebeke et al., 2005; de Groot et al., 2006). Although it has been a serious pest in homogeneous pine plantations throughout the Southern Hemisphere, the potential impact of *S. noctilio* in North America is not known and may be complicated by heterogeneous landscapes, diverse species composition and management practices, and a rich community of competitors and natural enemies (Dodds et al., 2010; Dodds & de Groot, 2012).

Sirex nigricornis is native to eastern North America (Schiff et al., 2012). The biology and ecology of *S. nigricornis* has not received much attention until recently, when *S. noctilio* arrived in North America. Study of *S. nigricornis* will further our understanding of its biology and ecology, and aid in prediction of the temporal interactions that it, or its natural enemies, might have with *S. noctilio* in North America. Adult siricids are ephemeral; they do not feed and live for only 3–14 days (Madden, 1974; Spradbery, 1977). Siricid females are facultatively parthenogenic, males develop from unfertilized eggs (i.e., arrhenotoky) (Rawlings, 1953; Morgan, 1968). Both *S. noctilio* and *S. nigricornis* are univoltine for most individuals in most areas of their respective ranges – or, at least in areas where *S. nigricornis* has been studied thus far (Morgan, 1968; Ryan et al., 2012a; Johnson et al., 2013).

Our objective was to determine whether emergence of both *S. noctilio* and *S. nigricornis* adults could be predicted by heat unit accumulation (degree days). Degree-day models for *Sirex* spp. can direct seasonal timing of research that requires study or capture of adult wasps, and may be useful for *S. noctilio* management practices in North America (e.g., silvicultural treatments, release of natural enemies) that may require knowledge of phenology in relation to heat unit accumulation. Models will also aid predictions of the distribution and population dynamics of *S. noctilio* under different climate scenarios.

Materials and methods

Adult emergence data

In southern Ontario, we identified pines (*Pinus sylvestris* L., *Pinus resinosa* Aiton, and *Pinus banksiana* Lamb.) infested with *S. noctilio* [4–23 cm diameter at breast height (dbh)] according to presence of fresh resin beads on the main bole indicating oviposition attack sites (from eight unmanaged pine stands, some were old Christmas tree plantations; details in Ryan et al., 2012b). Prior to woodwasp emergence (May – early-July of 2007, 2008, 2011, and 2012), we felled trees and moved 1-m-long infested logs to the Ontario Tree Seed Facility in Angus, Ontario (44.32°N, 79.87°W; 190 m elevation). We either cross-stacked the logs (i.e., log-cabin style) – so that there was minimal interference of wasp emergence – under a screened canopy (hereafter referred to as tent) or placed them individually in standing cardboard cylinders within a covered, unheated translucent-sided shed (hereafter shed; Ryan et al., 2012a; Table 1). Cardboard rearing tubes and tents were checked every few days prior to emergence, and once emergence began, 3–5 days per week. Wasps were collected, sorted according to sex, and counted.

In Louisiana, infested pine (*Pinus echinata* Mill., *Pinus taeda* L., and *Pinus palustris* Mill.) material (i.e., residual fresh crowns from a November 2008 logging operation) was collected during September to early-October 2009, and moved to a combination of conditioned and outdoor rearing facilities at the Alexandria Forestry Center (1.36°N, 92.43°W). In 2009–2011, rearing material was derived from trap trees (designed to mimic fresh logging crowns), created by felling live un-infested *P. taeda*, 15–20 cm dbh, in October and November, prior to peak flight of wild female *S. nigricornis*. Stems of felled pines were immediately bucked into 1.2 m lengths and stacked in alternating layers of rows of bolts (3–4), and left on site adjacent to residual crown material [2009–2012: Catahoula (31.60°N, 92.42°W); 2010: Johnson (31.16°N, 92.67°W), both in the Kisatchie National Forest] to be colonized by *S. nigricornis*. Prior to any woodwasp emergence the following year (September), trap tree bolts were moved to nearby rearing tents located under an open-sided pole-barn at the Catahoula Work Center (31.50°N, 92.46°W). Tents were checked for wasp emergence 3–4 days per week during peak emergence, and once or twice per week during early and late emergence. Wasps were collected, sorted according to sex, and counted.

Weather data

We obtained daily minimum and maximum temperatures for Ontario from Environment Canada, National Climate Data and Information Archive (www.climate.weatheroffice.gc.ca; accessed 27 November 2012), and for Louisiana from the National Oceanic and Atmospheric Administration (NOAA, www.ncdc.noaa.gov/cdo-web/; accessed 6 December 2012). Temperatures used to calculate cumulative degree days (CDD) for *S. noctilio* models were from the Barrie-ORO station (1 January 2007 – 10 September 2012; 44.48°N, 79.55°W; 289 m elevation), located 17 km northeast of Angus, Ontario. Temperatures used to calculate CDD for *S. nigricornis* models were from the NOAA weather station located at the Catahoula Work Center (1

Table 1 General information, including actual emergence dates, for *Sirex noctilio* (Ontario) and *S. nigricornis* (Louisiana) emergence data sets used to develop degree-day models or to test their predictive accuracy

Species	Data set	Condition	Year	Sex	n	10%	50%	90%
S. noctilio	Test	Shed[1]	2007	Males	1703	11 July	23 July	21 August
				Females	522	12 July	24 July	24 August
			2008	Males	2451	14 July	23 July	13 August
				Females	1001	17 July	30 July	27 August
	Model	Tent	2011	Males	1521	15 July	30 July	12 August
				Females	256	21 July	5 August	12 August
			2012	Males	519	9 July	20 July	23 August
				Females	203	10 July	23 July	27 August
		Shed	2012	Males	232	3 July	16 July	20 August
				Females	47	6 July	23 July	27 August
S. nigricornis	Model	Indoors[2]	2009	Males	152	15 October	26 October	4 November
				Females	137	21 October	30 October	9 November
	Test		2010	Males	80	19 October	29 October	10 November
				Females	113	25 October	5 November	22 November
	Model	Tent	2010	Males	397	16 October	24 October	10 November
				Females	266	19 October	1 November	15 November
			2011	Males	418	27 October	13 November	16 November
				Females	114	25 October	14 November	25 November
	Test		2012	Males	150	9 October	22 October	20 November
				Females	33	3 October	25 October	22 November

At least 1 month prior to emergence, all pine logs were placed outdoors in tents or sheds in Angus, Ontario (*S. noctilio*) or indoors, inside conditioned rearing boxes at the Alexandria Forestry Center, Pineville, LA (*S. nigricornis*) or tents at the Catahoula Work Center, Bentley, LA.

[1] Emergence data previously published in Ryan et al. (2012b).

[2] Pine logs kept at the Johnson site, near Alexandria, LA.

January 2009 – 30 November 2012; 70 m elevation), located 11 km southwest of the Catahoula site, and from the Alexandria International Airport (1 January – 24 November 2010; 31.33°N, 92.55°W; 36 m elevation), located 22 km northeast from the Johnson site.

Degree-day models

We used the program DEGDAY to calculate CDD (Zalom et al., 1983; available at: www.biomet.ucdavis.edu/DegreeDays/DegDay.htm). We chose the sine wave method of CDD calculation (Allen, 1976), whereby the temperature curve was approximated as a sine wave with minima and maxima defined by daily minimum and maximum temperatures, respectively. The sine wave method is preferable over the triangle method when minimum daily temperatures are at or below the developmental minimum (Pruess, 1983), which may be the case in early-spring (Higley et al., 1986). DEGDAY calculated the area under the temperature curve above and below the specified lower and upper threshold temperatures, respectively, providing heat units accumulated per day (Zalom et al., 1983; reviewed by Pruess, 1983 and Higley et al., 1986). Calculation of CDD began on a specified start date and ended on the date of 100% cumulative emergence for each respective woodwasp data set.

We chose several potential temperature thresholds for CDD calculation according to previously published reports of *Sirex* spp. phenology in North America (Ryan et al., 2012b; Johnson et al., 2013), and degree day or development literature on *S. noctilio* (Madden, 1981) and insects that develop in a similar habitat as woodwasps (i.e., subcortical beetles) (Akers & Nielsen, 1984; Bentz et al., 1991; Keena & Moore, 2010). Potential start dates for CDD included the first of the year (arbitrary), early-spring (near the end of winter quiescence), and late-spring (quiescence completed). We tested the start dates of 1 January, 1 April, and 1 May for *S. noctilio*, and of 1 January, 1 March, and 1 May for *S. nigricornis*. Spring begins earlier in Louisiana than in southern Ontario. Consequently, the early-spring start date was designated as 1 month earlier for *S. nigricornis*. For both species, 0, 5, 10, and 15 °C were tested as potential lower threshold (LT), and 25 and 30 °C as potential upper threshold (UT) temperatures.

Using JMP 10.0 (SAS Institute, Cary, NC, USA), we modelled cumulative *Sirex* spp. emergence against CDD.

We tried two types of sigmoidal functions, Gompertz and logistic, both with three and four parameters. A three-parameter Gompertz function provided the best fit to the data: Emergence (%) = a*exp{−exp[−b (CDD − c)]}, where a = asymptote, b = rate of increase, and c = inflection point. For *S. noctilio*, previously published data sets (2007 and 2008 in Ryan et al., 2012b) were used to test models developed with 2011 and 2012 emergence data (Table 1). For *S. nigricornis*, data sets with the largest sample sizes (2009–2011 from Catahoula) were used to develop models, and the remaining data sets [2010 from Johnson (hereafter 2010 J), 2012 from Catahoula] were used to test models (Table 1). We created separate models for males and females of each species, resulting in 24 iterations of each model (96 total iterations). Unique iterations were produced with different combinations of start date (n = 3), LT (n = 4), and UT (n = 2). We selected the best iteration of each model according to fit (R^2), minimization of error (root mean square error, RMSE), and how closely its predicted emergence matched actual emergence according to the test data sets (i.e., predictive accuracy). To measure predictive accuracy, we compared the deviation in emergence in actual days and the error in emergence (% of population emerged), between the test data sets (i.e., observed) and that predicted by models. Model fit and minimization of error were generally in agreement, although in some cases we selected models with better predictive accuracy over those with a slightly better fit and reduced error.

Results

Phenological patterns

Among four generations, emergence of *S. noctilio* in Ontario generally occurred from July through September, and emergence of *S. nigricornis* in Louisiana generally occurred from October through November (Table 1). For both *Sirex* spp., male emergence began before that of females (Table 1; mean ± SE of all data sets: *S. noctilio* 5 ± 2 days earlier, *S. nigricornis* 7 ± 2 days earlier). Cessation of emergence was variable between males and females among data sets (Table 1; mean of all data sets: males were 5 ± 6 days earlier and 1 ± 2 days later than females for *S. noctilio* and *S. nigricornis*, respectively).

Degree-day models

We selected a LT of 0 °C and an UT of 25 °C for degree-day models for both *Sirex* spp., because these temperature thresholds provided the best model fit and reduced error, and the best predictive accuracy among test data sets (Tables 2–4). A start date of 1 April for both male and female *S. noctilio* (Table 2, Figure 1) also provided the best model fit and reduced error, and the best predictive accuracy among test data sets (Table 3). For *S. nigricornis*, we selected a start date of 1 May and 1 March for males and females, respectively (Table 2, Figure 2). Although the model fit was slightly better and the error was reduced with a 1 May start date for female *S. nigricornis*, a 1 March start date was chosen because it provided the greatest predictive accuracy (Table 4).

A start date of 1 March for the female *S. nigricornis* degree-day model provided the best agreement among all five data sets. The 1 May start best described data sets used to develop the model (i.e., model fit), yet the 1 March start was better at predicting emergence among the data sets used to test the model (i.e., predictive accuracy). Specifically, CDD calculated with a start date of 1 May (10% emergence = 4 022 CDD; 50% emergence = 4 270 CDD; 90% emergence = 4 569 CDD) provided a better model fit and reduced error compared

Table 2 Parameter estimates of degree-day models for *Sirex noctilio* in Ontario and *S. nigricornis* in Louisiana. A three-parameter Gompertz function provided the best fit to the data; Emergence (%) = a*exp{−exp[−b(CDD − c)]}, a = asymptote, b = rate of increase, and c = inflection point

Species	Sex	Start date	R^2	RMSE[1]	a ± SE	b ± SE	c ± SE
S. noctilio	Males	1 April	0.91	9.7	103.3 ± 2.6	0.003 ± 0	1491.4 ± 12.7
	Females	1 April	0.86	11.3	115.0 ± 7.8	0.003 ± 0	1636.5 ± 33.5
S. nigricornis	Males	1 May	0.83	17.2	107.6 ± 5.5	0.005 ± 0.004	4142.2 ± 16.2
	Females	1 March	0.73	18.7	109.0 ± 9.1	0.004 ± 0.001	5241.8 ± 29.5
	Females	1 May[2]	0.85	14.1	111.3 ± 7.0	0.004 ± 0.001	4220.1 ± 20.0

All models were significant (F-test: P<0.001); models are identified by start date; lower thresholds were 0 °C, and upper thresholds were 25 °C for all four chosen models.

[1] RMSE, root mean square error.

[2] This model was a good fit with reduced error, but the 1 March start date was chosen as the best model because it provided better agreement among all five data sets, i.e., better predictive accuracy.

Table 3 *Sirex noctilio* emergence in Ontario as predicted from degree-day models (start date = 1 April, lower threshold = 0 °C, upper threshold = 25 °C for both males and females) in comparison with observed emergence from 2007 and that from 2008

	Males					Females				
		Predicted – observed					Predicted – observed			
		2007		2008			2007		2008	
Predicted emergence (%)	CDD[1]	Days[2]	%[3]	Days	%	CDD[1]	Days	%	Days	%
10	1239	−2	−11	1	3	1280	−5	−13	2	7
50	1587	−9	−25	−8	−24	1709	−14	−27	−7	−17
90	2081	−8	−7	−16	−9	2197	−10	−10	−10	−7

[1] CDD = cumulative degree days from the model start date until it reaches the target percentage of predicted emergence given in the first column.

[2] Positive number of days indicates emergence date predicted by model occurred earlier than observed, whereas negative numbers indicate that it occurred later than observed.

[3] Refers to the difference between the percentage of the population predicted to emerge by the model for each value of predicted emergence and that which had actually emerged according to the test data set (e.g., a 'predicted – observed emergence' value of −11% for a predicted emergence of 10% indicates that 21% of the population in the test data set had actually emerged).

Table 4 *Sirex nigricornis* emergence in Louisiana as predicted from degree-day models [start date = 1 May (males) and 1 March (females), lower threshold = 0 °C, upper threshold = 25 °C for both males and females] in comparison with actual emergence from the Johnson site in 2010 (logs kept indoors) and the Catahoula site in 2012 (logs kept outdoors in tents)

	Males					Females				
		Predicted – observed					Predicted – observed			
		2010		2012			2010		2012	
Predicted emergence (%)	CDD[1]	Days[2]	%[3]	Days	%	CDD[1]	Days	%	Days	%
10	3980	5	10	11	7	5016	9	10	−7	−11
50	4192	4	14	−8	−25	5306	6	23	1	5
90	4464	0	−4	3	1	5670	−2	−10	5	5

Given the different start dates, CDD are not comparable between models for male and female *S. nigricornis*; however, predicted emergence with start date = 1 May for *S. nigricornis* was 4022, 4270, and 4569 CDD for 10, 50, and 90%, respectively.

[1] CDD = cumulative degree days from the model start date until it reaches the target percentage of predicted emergence given in the first column.

[2] Positive number of days indicates emergence date predicted by model occurred earlier than observed, whereas negative numbers indicate that it occurred later than observed.

[3] Refers to the difference between the percentage of the population predicted to emerge by the model for each value of predicted emergence and that which had actually emerged according to the test data set (e.g., a 'predicted – observed emergence' value of 10% for a predicted emergence of 10% indicates that 0% of the population in the test data set had actually emerged).

with the 1 March date (Table 2). Compared to the 1 March start date (Table 4), however, the model developed with a 1 May start predicted 10% and 50% emergence poorly for the test data sets. The 1 May model predicted 10% emergence 8 days early, at 0% emergence for the 2010 Johnson data set, and 17 days late, at 27% emergence for the 2012 Catahoula data set. The 1 May model predicted 50% emergence 8 days early, at 27% emergence for the 2010 Johnson data set, and 9 days late, at 76% emergence for the 2012 Catahoula data set.

Effect of variation in temperature thresholds on CDD

For *S. noctilio*, model fit and error varied minimally among all temperature threshold inputs for CDD (R^2 = 0.91–0.95 and 0.86–0.89, RMSE = 6.7–9.7 and 10.0–11.2, for males and females, respectively). In contrast, model fit and error varied substantially for *S. nigricornis* among temperature threshold inputs for CDD (R^2 = 0.25–0.83 and 0.30–0.85, RMSE = 17.2–35.7 and 14.1–30.2, for males and females, respectively). For both *Sirex* spp., the largest differences in model fit and error

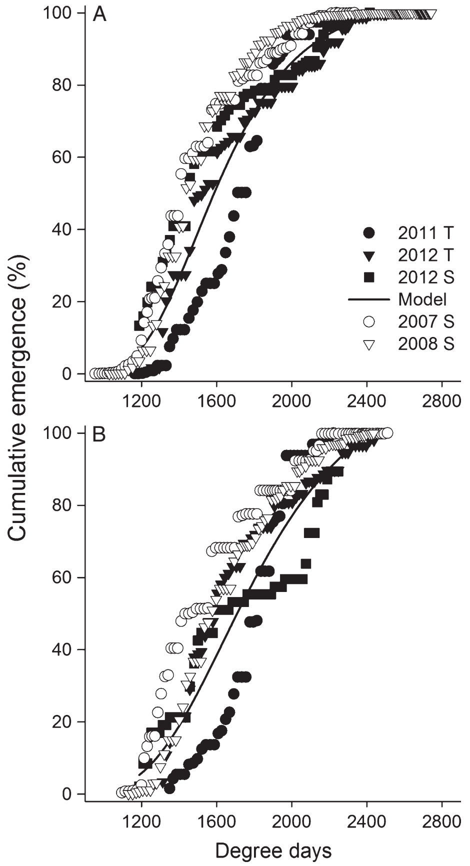

Figure 1 Degree-day models for *Sirex noctilio* (A) males and (B) females developed from cumulative adult emergence from pine logs in Angus, Ontario. Solid symbols represent data sets used to create models and open symbols represent data sets used to test models. Input parameters were: start date, 1 April; lower threshold, 0 °C; upper threshold, 25 °C for both males and females. Data sets are identified by year; S, logs kept in covered and unheated shed; T, logs crossed-staked under screened canopy.

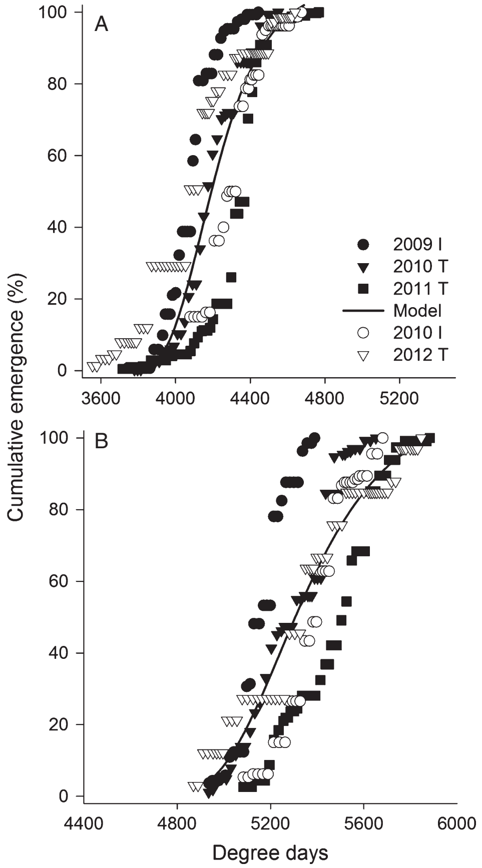

Figure 2 Degree-day models for *Sirex nigricornis* (A) males and (B) females developed from cumulative adult emergence from pine logs in the Catahoula Ranger District (Kisatchie National Forest), Louisiana. Solid symbols represent data sets used to create models and open symbols represent data sets used to test models. Input parameters were: start date, 1 May (A), 1 March (B); lower threshold, 0 °C and upper threshold, 25 °C for both males and females. Data sets are identified by year; I, logs kept indoors; T, logs kept outdoors in tents. Range on *x*-axis varies for (A) and (B), but scale is the same.

were among different LTs; increases in LT reduced model fit and increased error. Start date was also important; model fit was poor when CDD began on 1 January rather than on either of the spring start dates.

For both *Sirex* spp., the largest differences in predictive accuracy among temperature threshold inputs for CDD were among different LTs. The start date of 1 January always performed poorly compared to the spring ones (March, April, or May). Differences in predictive accuracy between the two UTs were small.

Predictive accuracy of models

Degree-day models for *S. noctilio* were most accurate at predicting 10% emergence and ranged from 2 days early when 3% of the population had emerged, to 5 days late when 23% of the population had emerged (Table 3, Figure 1). Degree-day models for *S. noctilio* were least accurate at predicting 50% emergence: range was 7 days late when 67% of the population had emerged, to 14 days late when 77% of the population had emerged (Table 3).

Degree-day models for *S. nigricornis* were most accurate at predicting 90% emergence, and ranged from 5 days early when 85% of the population had emerged, to 2 days late when 100% of the population had emerged (Table 4, Figure 2). Degree-day models for *S. nigricornis* were least accurate at predicting 10% emergence: range was 11 days early when 3% of the population had emerged, to 7 days late when 21% of the population had emerged.

Discussion

The degree-day models developed were relatively accurate in predicting emergence of *S. noctilio* in southern Ontario and *S. nigricornis* in Louisiana. The steepest portion of the cumulative emergence curve, near 50%, should have been the most difficult to predict, which was the case for *S. noctilio* (Table 3), but not for *S. nigricornis* (Table 4). Most difficult for degree-day models to predict was 10% emergence of *S. nigricornis* populations. This may be, at least in part, because *S. nigricornis* had a shorter, steeper emergence curve than *S. noctilio*. *Sirex noctilio* emergence occurred within a range of 1 350 (males) and 1 270 (females) CDD, whereas all emergence occurred within a range of only 1 050 (males) and 950 (females) CDD for *S. nigricornis* (Figures 1 and 2). Peak emergence for *S. nigricornis* took place among fewer calendar days than it did for *S. noctilio*, allowing degree-day models to predict 50% emergence more accurately for the former than for the latter. A steeper emergence curve for *S. nigricornis* compared with *S. noctilio* does not, however, explain why 90% emergence was easier to predict than 10% emergence for *S. nigricornis*; there was substantial variation among data sets at the beginning and at the end of the emergence curve (Figure 2).

Higley et al. (1986) suggest an acceptable error of 10–15% in predicting insect emergence when degree-day models are used to provide pest management recommendations, yet more accurate estimates of emergence may be necessary for studies of insect population dynamics. Errors from our models were below or within this margin for predicting 10 and 90% emergence (1–13%), but not for predicting 50% emergence (5–27%) (Tables 3 and 4). Because the start of emergence is often of greatest concern for management applications, these models could be used for such purposes. Errors could have been reduced by increasing power with larger sample sizes; some data sets used to test models were quite small ($n<100$ wasps). Frequency of wasp collection may have also improved model accuracy. Emergence was monitored more frequently for *S. noctilio* in Ontario than for *S. nigricornis* in Louisiana – model fits were better and error terms were smaller for *S. noctilio* degree-day models. Lastly, rearing conditions likely affected emergence timing. *Sirex noctilio* emergence began earlier when reared in covered sheds compared to tents (Table 1, Figure 1). For use in studies of *Sirex* population dynamics, these models would benefit from measures described above for reducing error as well as additional data acquired from different sites and years.

Our degree-day models do not reflect actual emergence of woodwasps from standing trees, and true timing of emergence under natural field conditions may vary somewhat from what we report. Our results are similar to those reported by Madden (1981) for *S. noctilio* reared under laboratory conditions. Madden (1981) found that 2 500 CDD were required for *S. noctilio* to complete development from egg to adult; we found that development was complete after 2 430 CDD from overwintering larva (1 April) to adult. Madden (1981) found that *S. noctilio* egg development was optimal at 25 °C – the same temperature we chose as the upper threshold for development. The lower threshold, 6–7 °C for *S. noctilio* of various life stages, reported by Madden (1981), was higher than the lower threshold that we chose (0 °C) for degree-day models.

In natural environments, factors other than temperature clearly influence *Sirex* spp. phenology. For instance, emergence timing may be related to daily weather conditions (i.e., sunny vs. overcast). Upon emergence, female *S. noctilio* are photopositive (Dolezal, 1967; Madden, 1974), and once emerged, they are inactive on cold, rainy days (Dolezal, 1967). A few cool, overcast days during peak emergence can result in cessation of emergence for up to 1 week (Morgan & Stewart, 1966). It is possible that adults wait inside trees for a sunny day to emerge, when mating and oviposition conditions are optimal, even if enough heat units have accumulated for development to be complete.

In conclusion, degree-day models can be used to predict timing of the adult flight period of *S. noctilio* in southern Ontario and *S. nigricornis* in Louisiana. Consistent with observations of *S. noctilio* phenology in the southern hemisphere (Morgan & Stewart, 1966; Taylor, 1981), we found that male emergence begins a few days prior to and concludes at about the same time as that of females for both *Sirex* spp. In southern Ontario, models predict that *S. noctilio* adults will be in flight between 1 015 and 2 430 CDD (using a 1 April start date; from early-July until mid-September). In Louisiana, models predict that *S. nigricornis* adults will be in flight between 3 854 and 4 700 CDD (using a 1 May start date; from early-October until late-November).

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