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Using plant volatile traps to develop phenology models for natural enemies: An example using Chrysopa nigricornis (Burmeister) (Neuroptera: Chrysopidae)

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For: *Biological Control*

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Running head: Phenology of *C. nigricornis*

Using Plant Volatile Traps to Develop Phenology Models for Natural Enemies: An example using *Chrysopa nigricornis* (Burmeister) (Neuroptera: Chrysopidae)

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Abstract. A model predicting phenology of adult *Chrysopa nigricornis* (Burmeister) (Neuroptera: Chrysopidae) in orchards was developed from field (trapping) data supplemented with development data collected under laboratory conditions. Lower and upper thresholds of 10.1°C and 29.9 °C, respectively, were estimated from published and unpublished laboratory observations, and were used to develop a phenology model. Season-long field data were collected using white delta traps that had been baited with squalene, a volatile shown previously to be highly attractive to *C. nigricornis*. The model was developed from data collected in three Washington apple orchards, and was validated using independent data sets collected from apple, sweet cherry, pear, and walnut orchards over a 2-4 year period across a much wider geographic region. We found that the mean absolute deviation across all crops and years was 39.7 ± 1.2 day-degrees (DD), or 4.4 ± 0.14 days. Populations of *C. nigricornis* from walnut orchards in California emerged 105 DD later than those in Oregon and Washington, thus requiring correction of average time of first trap catch in California to synchronize models. The ability to use a single model across multiple crops, different prey species and abundances, and different pesticide regimes demonstrates that phenology models for generalist predators may have broader application to IPM programs in other cropping systems.

Keywords: Chrysopa nigricornis; phenology model; herbivore-induced plant volatiles; apple; walnut; pear; sweet cherry

1. Introduction

Phenology models for pests have dramatically changed pest management approaches in a broad range of agricultural systems. Fundamentally, the ability to predict pest phenology allows a shift from a reactive management strategy to one in which management decisions can be planned well ahead of the dates when management activities are actually needed (Croft *et al.*, 1976; Gage *et al.*, 1982; Welch *et al.*, 1978). Phenology models are based on the idea that the duration of various developmental stages of insects and mites (and other poikilothermic organisms) can be predicted by temperature accumulations above some lower temperature at which development rates are zero, and below an upper threshold at which development is prevented because of thermal deactivation of certain physiological processes (Jones, 1991).

One of the first phenology models developed in pest management was for the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). Landmark studies in the mid-to-late 1920's gave detailed information about the developmental of codling moth at various temperatures (Garrett, 1922; Glenn, 1922a; Glenn, 1922b; Shelford, 1929). This information was used to devise a cumbersome method for calculating heat accumulations, but the method was never widely adopted. Technological and computational improvements in the 1970's allowed scientists to re-visit phenology models for codling moth and a variety of other pest insects (Gage *et al.*, 1982; Riedl and Hoying, 1980; Riedl *et al.*, 1979; Riedl *et al.*, 1985; Welch *et al.*, 1978) and helped IPM managers time key management activities (Gage *et al.*, 1982; Welch *et al.*, 1978).

While phenology models for pests have matured and entered the mainstream of IPM tactics, the

development of phenology models for natural enemies have not progressed at the same rate. Although there are a number of studies on the temperature dependent development for natural enemies, there are far fewer models than might be expected given the success of degree-day models for pests in IPM programs. Part of the discrepancy is likely the result of the greater difficulty in rearing and performing development rate studies on natural enemies because of the need for rearing prey or host species in addition to the predator or parasitoid species. An additional complication has been the difficulty of sampling natural enemies quickly, and with sufficient precision and numbers for model development and validation studies. Given the diversity of natural enemies that occur in even the simplest agro-ecosystem, and the need for development rate data at multiple temperatures (so that developmental thresholds can be estimated), it is not surprising that only a few natural enemy models have been developed, validated and used for management purposes.

Major advances in the development of phenology models for both pests and natural enemies have come from a series of papers that evaluated development rates and temperature thresholds for a broad range of arthropods. These studies have revealed several key findings that simplify model development: (1) Insects and mites exhibit development rate isomorphy, where the proportion of total development time spent in a particular life stage does not change with temperature (Jarošík *et al.*, 2002; Jarošík *et al.*, 2004). This means that the lower development threshold (LDT) is constant among life stages within a species, which allows the use of a single stage (e.g., eggs or pupae) to estimate the LDT for a species. In addition, this also means that if the development times for all stages for a given temperature are known, comparable development times for other temperatures can be estimated from only a single life stage, which

greatly simplifies laboratory studies. (2) The range of temperatures between the upper and lower thresholds for development of 66 species of insects in 8 different orders averaged 19.8°C ± 0.7 ($\bar{x}$ ± 95% CI) (Dixon *et al.*, 2009). Therefore, once the lower threshold is determined, the upper threshold can be estimated and tested against field data for accuracy.

The final advance that should accelerate the development of phenology models for natural enemies comes from research performed over the past 10-15 years on the use of herbivore-induced plant volatiles (HIPV)/floral volatile dispensers to evaluate whether natural enemy population abundance and spatial distribution can be manipulated to improve biological control (James, 2003a; James, 2003b; James, 2005a; James, 2005b; James and Price, 2004; Kahn *et al.*, 2008; Toth *et al.*, 2006; Toth *et al.*, 2009; Turlings and Ton, 2006; Yu *et al.*, 2008; Zhang *et al.*, 2006). These studies and more recent ones (Jones *et al.*, 2015; Jones *et al.*, 2011; Rodriguez-Saona *et al.*, 2011) have shown that when paired with traps, HIPV/plant volatile lures can be used to monitor a broad range of natural enemies and provide information on their abundance, diversity, and phenology that would be useful for IPM programs.

In this paper, we focus on the use of a volatile HIPV lure to develop a phenology model for adults of the green lacewing *Chrysopa nigricornis* Burmeister (Neuroptera: Chrysopidae). This species has a transcontinental distribution in North America, extending as far south in the U.S. as New Mexico and Texas, and northwards into most of the Canadian provinces (Garland and Kevan, 2007; Penny *et al.*, 1997). *Chrysopa nigricornis* has a distinct preference for deciduous trees and shrubs over herbaceous vegetation (Horton *et al.*, 2009; Petersen and Hunter, 2002; Putman, 1932), and is a common predator of aphids and other soft-bodied arthropods in fruit and

nut orchards throughout North America (Szentkirályi, 2001). The species has 2-3 generations per year in the western U.S. (Carroll and Hoyt, 1984; Horton *et al.*, 2012; Toschi, 1965), overwintering in diapause as a cocooned last-instar larva (Tauber and Tauber, 1972) in bark crevices or beneath plant litter. The seasonal activity of adults under Pacific Northwest conditions can be quite prolonged, and may extend from early-May well into October (Garland and Kevan, 2007).

The few quantitative studies that address *C. nigricornis* phenology almost exclusively examine the larval stage (Carroll and Hoyt 1984, Horton et al. 2012). Here, we demonstrate that a volatile attractant (squalene; Jones et al. 2011) can be used under orchard conditions across a broad geographic range to monitor flight phenology of *C. nigricornis*. We used trap catch data in combination with development rate data for this species to develop a temperature-based phenology model for *C. nigricornis* in fruit and nut orchards of Washington, Oregon, and California. Our objective was not only to develop an effective phenology model for this species, but also to evaluate how phenology models for natural enemies in general may highlight areas where additional research is needed in our efforts to maximize conservation biological control.

2. Materials and Methods

2.1 Lure Construction

Lures were made using 5 cm wide x 7.5 cm long sections of polyethylene tubing (Associated Bag Company, Milwaukee, WI). The tubing was heat sealed at one end and a 3.8 cm long piece of dental wick was placed into the bag, and 1 ml of squalene (Sigma-Aldrich, St. Louis, MO)

was applied to the wick before heat-sealing the other end of the bag (Jones *et al.*, 2011).

2.2 Orchards and Traps

We sampled apple, pear, cherry, and walnut orchards in California, Oregon and Washington during the growing seasons of 2009-2013. We used four replicate traps in each orchard, spaced > 100m apart. Lures were placed in the large white plastic delta traps that are commonly used for monitoring codling moth in Western Orchards (Suterra LTD, Bend, OR) or above white panel traps (Alpha Scents Inc., West Linn, OR, USA) for the years after 2010.

Data from California consisted of 3 walnut orchards each year sampled from mid- March to mid-October. In 2009, orchards were in Yolo, Solano, and Fresno counties, but in 2010-11 were only in Yolo (2) and Solano (1) counties. In 2009, sampling in the Fresno orchard was terminated on 14 July.

Oregon orchards were a mixture of pear and sweet cherry orchards. There were three sweet cherry orchards sampled in each of 2010 and 2011 and they were in Hood River (1) and Wasco (2) counties. In 2010 the sampling started in early May (5-7) and continued until 15 September, while in 2011, sample collections started in late March (23-30) and continued to 13 September. The pear sampling in 2009-2011 consisted of five orchards sampled in Hood River County from 20 March to 30 October (2009), 25 Feb-30 Sept (2010) and 17 March-26 October (2011).

Washington data came from the Yakima and Wenatchee growing regions and varied considerably between areas. In the Yakima area during 2009 there were five apple orchards

sampled, with one orchard sampled from 26 March to 19 October, the other four were sampled starting in early to mid-June (4-15) and continuing to mid-late September (16-30). In 2010, there were four apple orchards that were sampled from late March (22-30) to early October. There were only three orchards (all pear) sampled from 16 March to 28 September in 2011. All the Yakima area orchards were in Yakima County.

The Wenatchee area orchards were a mixture of apple and sweet cherry orchards. There were three sweet cherry orchards sampled in 2010-2011 one each in Chelan, Douglas, and Grant counties. All the cherry orchards were sampled from mid-March (11-15) to the end of September in 2010 and from 17-28 March to 14 September in 2011. Five apple orchards were sampled in 2009 (four in Grant county, one in Douglas county) from 20 March-20 October at four of the sites, and at the other two sites from 2 June to 17 September. In 2010, there were four apple orchards (two in Douglas and two in Grant counties) sampled from 11-16 March to 21-25 October; in 2011 there were nine apple orchards sampled from March 28-April 14 to 6 October (five in Douglas county, four in Grant county). The 2012 orchards were the same orchards as in 2011, and were sampled from 20 March to 27 September. Fourteen apple orchards were sampled in 2013 between 22 March-3 April and 8-10 October.

2.3 Development rate and temperature thresholds for *C. nigricornis*

Development rate data for *C. nigricornis* were obtained from an unpublished manuscript (Fye, 1984), from literature sources (Petersen and Hunter, 2002; Tauber and Tauber, 1972), and from the results of recently completed laboratory studies (A Gadino, and VP Jones, unpublished) (Table 1). We used linear regression to examine the development rate of the immature stages

(development time^{-1}) as a function of temperature, for estimating the LDT (-intercept/slope) and the sum of effective temperatures (SET) or degree-days required to complete development (slope^{-1}) (Arnold, 1959).

2.4. Phenology Model Development and Validation

The data set used for model development was collected from the two Wenatchee area apple orchards and the one Yakima apple orchard that were sampled season-long in 2009. These data were chosen for use in model development because the data collection was more extensive at those locations. Traps at these three sites were collected and examined every 3-4 days throughout the growing season, whereas in the model validation data set traps were inspected at weekly intervals. While the difference in trap checking frequency causes the resolution of the model development data set to be greater (≈ 2x; 1.75 d versus 3.5 d), the random nature of when sampling occurred (on a DD scale) and variability in environmental conditions at any given location/sampling interval would be unlikely to bias the error rates compared to using exactly the same sampling intervals. Initial analysis using an interpolation of trap catch for each sampling interval did not affect validation results. For each generation of *C. nigricornis*, the relationship between the cumulative proportional trap catch data from this data set and degree-days was fit to a Weibull distribution (Wagner *et al.*, 1984) as described below.

For model validation, data from a particular location and generation were excluded if the trapping either started too late or if it ended too early (i.e., if we missed >20% of the adult flight period based on DD accumulations), or if the total number of lacewings trapped within a generation was <25 specimens. We were concerned that either factor could result in distortion of

the cumulative flight curve. For model validation, our focus was to not only to evaluate the apple-based phenology model (using apple data collected in other locations and years than used for model development), but also to evaluate how well the apple-based phenology model worked for the more limited data collections from sweet cherry, pear, and walnut orchards.

Daily maximum and minimum temperature records were collected at each orchard location, or were obtained from the nearest weather station through either the UC IPM weather network (California), the IFP network (Oregon), the WSU-AgWeather Net (Washington), or from the NOAA National Digital Forecast Database (NOAA, 2012) archive. Degree-day (DD) accumulations in degrees Celsius were calculated using a 10.1 °C lower threshold using the single-sine method with a 29.9°C horizontal cutoff (Baskerville and Emin 1969) and began on 1 January.

A critical part of the model development was the assignment of each trap catch interval to a particular generation. Strictly speaking, as the phenology model was developed from trap catch data, it predicts the seasonal timing of trap catch rather than emergence of lacewings from the pupal stage. Thus, in addition to the SET for *C. nigricornis*, the timing of trap catch could also be influenced by adult longevity, and possible differences between the temperature where the insect occurred in the field and the air temperature that was used to drive the model. We therefore used the laboratory data on SET to approximate when the cutoffs would likely occur between generational flight periods, while acknowledging that there likely is to be overlap between them.

Once the cutoffs for the generational flight periods had been assigned, the cumulative proportional trap catch data from each of the three orchards used in the initial apple data set were fitted to the accumulated degree-days for these locations using a Weibull distribution. We used the pweibull function in Stata 13.0 (Statacorp, 2013) to perform a weighted maximum likelihood fit of the data for each generation to the cumulative Weibull function (Wagner *et al.*, 1984):

$$y = 1 - \exp(DD/b)^c \quad (1)$$

where *y* is the empirically observed cumulative proportional trap catch, DD is the observed degree-day accumulation, *b* is a scale parameter in DD, and *c* is a shape parameter. The trap catch data used in fitting the model were restricted to the center 95% of the observed cumulative proportional trap catch for a given generation, to prevent the tails of the distribution from having undue influence of the shape of the curve. Using the center 95% of the distribution curve also helped minimize the potential problems associated with the overlap of generations.

Once the Weibull distribution had been fit to the cumulative proportional trap catch data for the initial apple data set, we used the model to predict the complete flight curve for each generation and to graphically compare the fit of the apple-based phenology model to the cumulative proportional trap catch data from all orchards in a particular geographic region combined for each of the different crops represented in the validation data set. We also used the Weibull parameters of the phenology model developed from the initial apple data set to estimate the DD at which the observed cumulative proportional trap catch occurred for each generation/location using a re-arrangement of the Weibull model (equation 1).

$$DD_{predicted} = b * \left(\ln(1 - y)^{\frac{1}{c}}\right) \quad (2)$$

This predicted value was then used to calculate the mean absolute deviation (MAD) (Quinn and Keough, 2008) in DD between when a particular proportion of trap catch was observed in the validation data set and what the model predicted for each crop and geographic area (*i.e.*, MAD= $\frac{\sum_{i=1}^{n}|observed_i - predicted)|}{n}$). The MAD was calculated separately for each crop and geographic location but pooled over years to evaluate whether model performance was relatively constant or varied by crop and broad geographical distribution. We also compared the Julian date at which a particular cumulative proportion trap catch occurred and the Julian date when it was predicted to occur using the DD accumulations (eq. 2), again using the MAD. All summary statistics comparing the predicted and observed data set omitted the dataset used to fit the apple model because it would be expected that the fit to the developmental data should be better than for the validation data set, and thus skew the apple validation results towards a lower error rate. When discussing the MAD error rates, measures of variability used were all either DD ± SEM or days ± SEM.

3. Results:

3.1. Development rate and temperature thresholds for *C. nigricornis*

An unpublished manuscript (Fye 1984) contained information on the development rate of *C. nigricornis* at temperatures between 12.5 and 33.3 °C (Table 1). Temperature data of 24 and 27 °C were also available from Tauber and Tauber (1972) and Petersen and Hunter (2002), respectively. We focused on the development rate over the egg-adult period, and found that the

data showed the expected decrease in development time as temperature increased, but that variability increased at the higher temperatures. A plot of development rate (development time^{-1}) versus temperature showed that there was a linear relationship over the 12.5-30 °C range and that the LDT was 10.1 °C. The SET for all immature stages combined was 385 DD ± 8.7 (Table 1). The development data of Fye (1984) suggested that the upper developmental threshold occurred near 30°C (Table 1); we chose 29.9 °C based on the work by Dixon et al. (2009) that showed on average the upper threshold was 19.8°C higher than the LDT.

C. nigricornis overwinters as a pre-pupa in a silk cocoon (Tauber and Tauber, 1972). The first trap capture for the three orchards in the initial apple data used for development of the phenology model was at 102.8 DD ± 1.7, which was earlier than expected based on the 179 DD required for completion of the pupal stage from the laboratory data (Table 1). However, *C. nigricornis* often overwinters under the bark of tree trunks, and so solar heating of the trunks would provide a different level of heat accumulation than would be predicted solely by air temperature. Our estimated overwintering generation cutoff was the initial flight time (100 DD) + the mean developmental time (385 DD) or 485 DD. Later flight cutoffs occurred at 385 DD intervals.

3.2 Phenology model development

The data from the three apple orchards in 2009 showed that we could have up to three flights (the overwintering generation and two summer generations), which could have considerable overlap because of the long adult lifespan of *C. nigricornis* (Gadino & Jones, unpublished). The Weibull model fit all three adult flights well (Fig. 1). The parameter estimates of the model for the three

successive flights were b_1 = 300.7 ± 1.6 and c_1 = 3.59 ± 0.05, b_2 = 721.7 ± 1.9 and c_2 = 9.04 ± 0.16, and b_3 = 1090.2 ± 1.3 and c_3 = 13.06 ± 0.15, respectively. The overall error rate (MAD) for the phenology model, based on this initial apple data set was 27.1 DD ± 2.6 or 2.6 d ± 0.3 (Table 2). The MAD errors on both a DD and a calendar date basis tended to be higher in the second flight at the Wenatchee locations, probably because that is the general time that sprays for codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) begin. The Yakima location did not show significant differences in accuracy between flights, but this orchard is an experimental orchard managed by USDA-ARS and had no sprays applied in 2009 for control of any insects, so that any pesticide-induced changes in phenology would not have occurred.

3.3 Phenology model validation

There were a total of 83 apple flights (30, 26, 27 orchard/years for flights 1-3, respectively), 24 flights for sweet cherry (6, 8, 10 orchard/years for flights 1-3), 24 flights for pear (7, 10, 7 orchard/years for flights 1-3), and 13 flights for walnut (5, 5, 3 orchard/years for flights 1-3) in the validation data set. The validation data from the apple orchards in both Wenatchee and Yakima had higher error rates than the initial apple data used to develop the model with an overall MAD of 40.4 DD ± 1.8 /4.4 d ± 0.21 in the Wenatchee area and 34.9 DD ± 3.0 /4.9 d ± 0.51 in the Yakima area (Table 2). The error rates on a DD scale were lowest in the first flight and similar between flights 2 and 3; on a calendar date basis, errors were greatest in the first flight (Table 2). Evaluation of the fit of the model for apple showed some variation from year to year, but nothing that would suggest systematic departures from the model (Fig. 2).

Results from the walnut orchards in California showed that the first trap catch occurred an average of 105 DD later than the trap catch in apple, pear, and sweet cherry orchards in Washington and Oregon. Thus, the use of the raw DD accumulations from 1 January in California resulted in relatively large errors for the phenology model, particularly for the first and second flights. To reduce error rates, we reset the DD accumulations to the same DD scale as used for Washington and Oregon by subtracting the average difference in first trap catch (105 DD) from California DD estimates. Once the DD corrections were made, the overall MAD error rate was 38.4 DD ± 3.7 /3.5 d ± 0.32 (Table 2). The largest departures for the model were for the second flight in 2011 (Fig 3). This variability was not seen in the 2009 data (Fig. 3) and insufficient numbers were caught at any location in 2010 to evaluate causes. However, further examination of the data showed that lures had been changed the week before the trap catch spiked at both locations in 2011, suggesting that the issue with the second generation flight in 2011 was related to lure performance. For the most part, the walnut orchards were not sprayed with insecticides, except for late in the season (after the third flight) in 2010-2011 at one location.

Data from sweet cherries had an average model error rate that was about 8 DD /0.9 d larger than that from the validation data for the apple orchards (Table 2). The Wenatchee data had slightly more error on a DD scale, but slightly less error on the calendar date scale (overall MAD error 50.9 DD ± 4.8 /5.3 d ± 0.61) compared to the Oregon data (overall MAD error 43.2 DD ± 4.7 /5.5 d ± 0.56) (Table 2), primarily because of results from the second flight (Fig. 4). The differences in error between the calendar and DD scale are a result of the different temperature profiles in the two areas. Spray programs for powdery mildew, black cherry aphid (*Myzus cerasi*

(F.), Homoptera: Aphididae), and western cherry fruit fly (*Rhagoletis indifferens* Currant, Diptera: Tephritidae) all began in the latter part of the first flight period and typically ended by the start of the third flight, so some of the variability seen in flight two is likely pesticide-related.

The fit of the phenology model for *C. nigricornis* in pear orchards was slightly better than was observed in apple (Table 2, Fig. 5). Insecticide applications directed at pear psylla, *Cacopsylla pyricola* (Förster) (Hemiptera: Psyllidae) in both Oregon and Washington pear orchards were frequent during the first flight through the start of the second flight, but there was not a clear pesticide-induced effect on phenology other than the near complete suppression of trap catch during a flight; when less than 25 individuals were caught, they were excluded from the analysis.

4. Discussion

In each of the tree crops surveyed, the prey complex used by *C. nigricornis* was different in terms of species, abundance, seasonal phenology, and nutritional value, and yet a single model provided good predictions of *C. nigricornis* seasonal phenology. There were differences in the abundance of lacewings caught in the HIPV-baited traps, with the general trend being the higher the latitude, the greater the numbers caught, but the seasonal timing on a DD scale was similar between locations, crops, and years. In addition to the differences among prey in each of the tree crops surveyed, the different pesticide use patterns and broad geographical distribution of orchards used in our studies, further suggest that for *C. nigricornis* as a generalist predator, the phenology model can be relatively robust. In general, the pesticide effects on phenology in our data (at any specific location) were either a general reduction in the numbers caught or near complete suppression of a particular flight. Landscape-level movement and re-invasion of the

orchards from external sources likely makes the phenology much more stable than if *C. nigricornis* was restricted solely to a particular orchard, its supply of potential prey, and disruptions from pesticides. For example, movement into the orchard from unsprayed habitats would mask reductions in lacewing populations within the orchard from pesticide applications. Although our model for *C. nigricornis* would best be described as one developed and validated in apple orchards, the data from sweet cherry, pear, and walnut show no systematic departures in phenology (other than the timing of the first flight in California) that would limit model usefulness in those crops. If these findings apply similarly to other generalist predator species (as suggested by unpublished data for two syrphid fly species collected in our project), then a phenology model developed for a particular natural enemy in one crop should provide a useful foundation for IPM programs in other cropping systems.

The California data showed that enough heat units were accumulated for a fourth flight of *C. nigricornis*. However, there were comparatively few orchard/years worth of data showing the fourth flight so that we could not both fit a model for the fourth generation and validate the resulting predictions. A partial fourth flight of *C. nigricornis* also occurred in apple orchards in the Wenatchee area in 2009. Examination of the diapause induction data from Tauber & Tauber (1972) suggests that if the critical photoperiod for diapause induction is the same in the western region as it was in the eastern region, then it would be likely that the number of flights occurring before the onset of diapause would be limited by differential heat unit accumulations in the different regions included in our study.

The most significant difference in the phenology data for *C. nigricornis* that we found in this study, was that between the timing of the first trap catch in California versus Washington and Oregon. The reason for this difference may be related to diapause termination/intensity, but the latitudinal pattern appears to resemble what Jones et al (2013) found in their geographically-based summary of the timing of first trap catch for codling moth. Jones et al. (2013) documented that emergence of codling moth occurred later (and predictably) on a DD scale at lower latitudes, such as California, and low elevations compared to those at higher latitudes. A reduced level of chilling is expected at lower latitudes and is known to affect the subsequent time to emergence from overwintering of a number of insect species (Leather *et al.*, 1993; Tauber *et al.*, 1986). Our observations on the timing of first trap catch of *C. nigricornis* appear to fit this same pattern, suggesting that diapause termination/intensity may also influence emergence from overwintering of this generalist predator.

An added value of the trap catch-based phenology model for *C. nigricornis* is that early in the season few or no lacewings were present before 100 DD at any location (205 DD in California). This provides a window in time when different pesticide applications can be made in tree fruit orchards in the western region without disrupting *C. nigricornis* populations. Later in the season, the flights overlap and finding a gap between flights for pesticide treatments would be difficult. However, having the phenology defined allows us to develop population models that can simulate the lethal or sub-lethal effects of pesticides applied at different times of the season on population development. Thus, defining the phenology is only the first step needed in optimizing conservation biological control efforts. Even without the population models, the use of squalene-baited traps in conjunction with phenology model predictions for *C. nigricornis* can

provide IPM practitioners with an estimate of the extent to which biological control is likely to contribute to the management of secondary pests in tree crops in the context of different management alternatives. In addition, when combined with trapping for *C. nigricornis* in adjacent unmanaged areas, this could help to identify and quantify potential source populations for movement into an orchard.

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Table 1. Development times for *Chrysopa nigricornis* from three different sources.

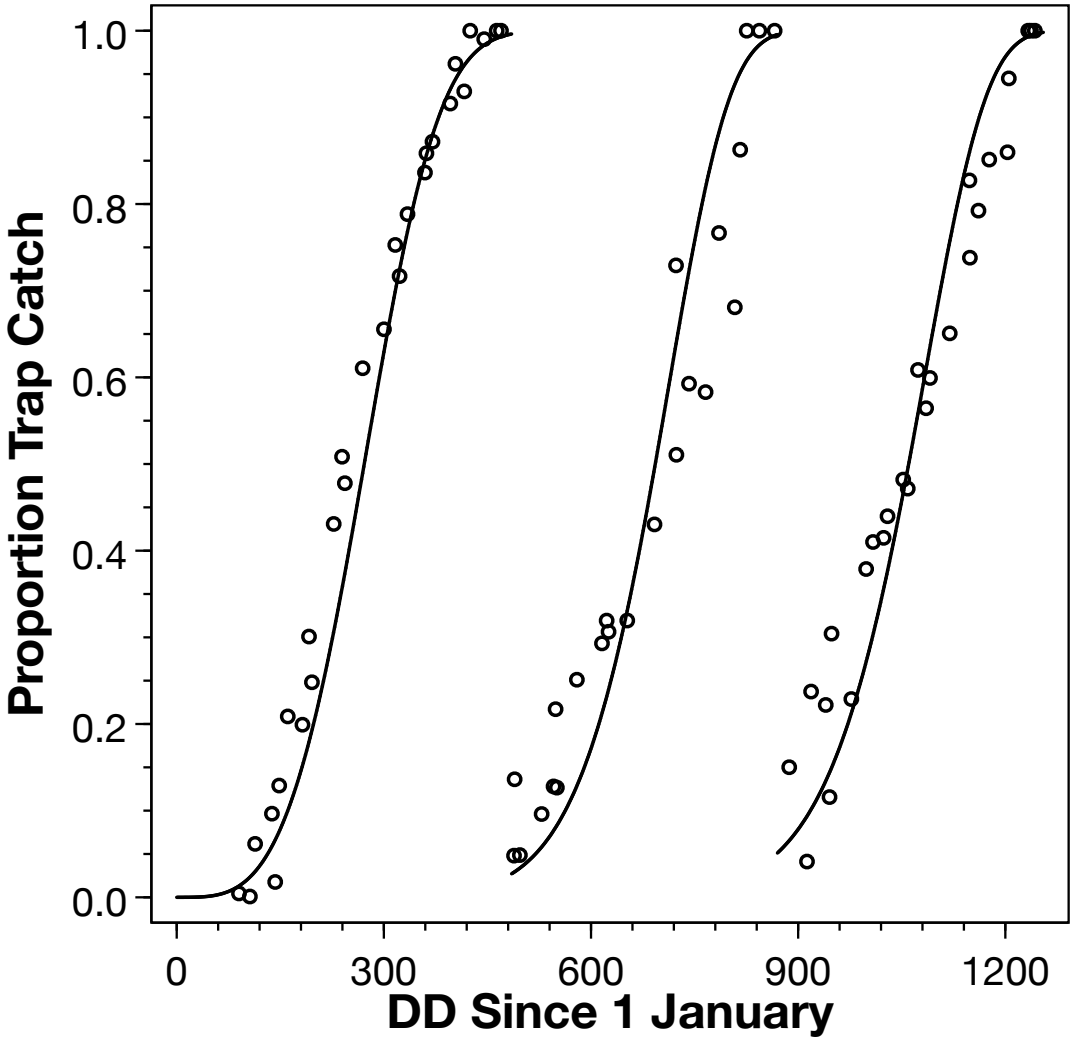
	Developmental time (days ± SD) for different stages of *C. nigricornis*							
Temp °C	Egg	L1	L2	L3	Pupa	Egg-Adult	Pre-oviposition period	Source
12.5	15.8 ± 1.8	12.6 ± 5.0	9.8 ± 1.6	13.9 ± 1.5	82.3 ± 11.9	134.3	–	Fye (1984)
15	14.8 ± 2.5	9.6 ± 1.3	9.0 ± 1.9	9.8 ± 2.4	47.3 ± 5.3	81.5	–	Fye (1984)
20	5.6 ± 0.7	4.4 ± 1.4	4.1 ± 2.2	5.3 ± 2.1	19.5 ± 13.1	38.9	–	Fye (1984)
24	4.3 ± 0.4	2.9 ± 0.4	2.6 ± 0.7	4.3 ± 0.7	9.25 ± 0.5	28.3	–	Tauber and Tauber (1972)
24	–	–	–	–	–	–	6.4 ± 1.8	Gadino and Jones (unpublished)
25	4.7 ± 0.4	3.0 ± 0.5	2.3 ± 0.5	3.8 ± 1.1	9.25	26.9	–	Fye (1984)
27	3.2 ± 0.7	2.2 ± 0.7	1.8 ± ± 0.7	2.7 ± 0.7	10.2 ± 0.7	20.1 ± 0.7	4.7 ± 0.4	Petersen and Hunter (2002)
30	3.0 ± 0.3	2.1 ± 0.4	2.2 ± 0.8	2.9 ± 0.8	9.5 ± 0.8	19.7	–	Fye (1984)
33.3	2.8 ± 0.1	2.1 ± 0.3	1.8 ± 0.5	4.0 ± 1.5	9.3 ± 1.1	20.0	–	Fye (1984)
Ave DD	58.3 ± 4.3	40.7 ± 2.1	36.1 ± 2.8	50.5 ± 3.5	178.6 ±13.5	387.2 ± 11.9		

Table 2. Model error by crop, geographic region, and generational flight for both the model development and model validation data sets.

		Mean absolute deviation error in days				Mean absolute deviation error in DD			
Crop	**Area**	**Flight 1**	**Flight 2**	**Flight 3**	**Overall**	**Flight 1**	**Flight 2**	**Flight 3**	**Overall**
Model Development Data									
apple	Wenatchee	2.2 ± 0.42 (14)*	3.5 ± 0.69 (15)	1.9 ± 0.39 (18)	2.5 ± 0.31 (47)	16.4 ± 2.8	39.6 ± 6.4	28.0 ± 4.9	28.2 ± 3.1
	Yakima	2.7 ± 0.61 (6)	2.7 ± 0.67 (3)	3.0 ± 1.2 (4)	2.8 ± 0.44 (13)	21.4 ± 6.3	26.7 ± 3.8	22.9 ± 7.5	23.1 ± 3.6
	both	2.3 ± 0.34 (20)	3.4± 0.58 (18)	2.1 ± 0.38 (22)	2.6 ± 0.26 (60)	17.9 ± 2.7	37.5 ± 5.4	27.1 ± 4.2	27.1 ± 2.6
Model Validation Data									
apple	Wenatchee	4.8 ± 0.37 (119)	3.8 ± 0.32 (77)	4.2 ± 0.33 (91)	4.4 ± 0.21 (287)	28.4 ± 1.9	49.7 ± 3.8	48.3 ± 3.4	40.4 ± 1.8
	Yakima	6.6 ± 0.93 (26)	3.9 ± 0.73 (14)	3.5 ± 0.55 (20)	4.9 ± 0.51 (60)	33.0 ± 3.4	45.5 ± 9.9	29.9 ± 3.7	34.9 ± 3.0
	both	5.1 ± 0.35 (145)	3.8 ± 0.29 (91)	4.1 ± 0.29 (111)	4.5 ± 0.19 (347)	29.2 ± 1.7	49.1 ± 3.6	45.0 ± 3.0	39.5 ± 1.6
sweet cherry	Hood River	5.9 ± 0.97 (16)	3.6 ± 0.79 (10)	6.3 ± 0.95 (16)	5.5 ± 0.56 (42)	30.7 ± 5.2	43.5 ± 10.0	55.4 ± 8.7	43.2 ± 4.7
	Wenatchee	6.5 ± 1.7 (11)	5.8 ± 0.86 (12)	4.3 ± 0.76 (20)	5.3 ± 0.61 (43)	40.9 ± 8.2	69.4 ± 10.3	45.3 ± 6.3	50.9 ± 4.8
	both	6.1 ± 0.88 (27)	4.8 ± 0.63 (22)	5.2 ± 0.61 (33)	5.4 ± 0.41 (85)	34.9 ± 4.6	57.6 ± 7.6	49.8 ± 5.2	47.1 ± 3.4
pear	Hood River	4.1 ± 0.89 (25)	3.4 ± 0.53 (31)	3.6 ± 0.74 (23)	3.7 ± 0.41 (79)	33.0 ± 6.1	32.2 ± 4.5	33.1 ± 4.5	32.7 ± 3.2
	Yakima	4.6 ± 0.58 (12)	5.8 ± 1.60 (9)	4.3 ± 0.78 (7)	4.9 ± 0.59 (28)	31.4 ± 3.8	61.2 ± 19.0	42.7 ± 7.5	43.8 ± 6.8
	both	4.3 ± 0.63 (37)	4.0 ± 0.55 (40)	3.7 ± 0.59 (30)	4.0 ± 0.34 (107)	32.5 ± 4.3	38.7 ± 5.7	35.3 ± 5.5	35.6 ± 3.0
walnut	California	4.4 ± 0.50 (31)	3.8 ± 0.61 (32)	3.5 ± 0.73 (18)	4.0 ± 0.35 (81)	33.0 ± 3.7	41.0 ± 7.3	43.3 ± 8.2	38.4 ± 3.7
All Validation Data		5.0 ± 0.26 (240)	4.0 ± 0.23 (185)	4.2 ± 0.23 (195)	4.4 ± 0.14 (620)	30.8 ± 1.4	46.5 ± 2.7	44.2 ± 2.3	39.7 ± 1.2

*Mean ± SEM. N is in parentheses and represents the number of data points evaluated per flight

Figure1


Proportion Trap Catch
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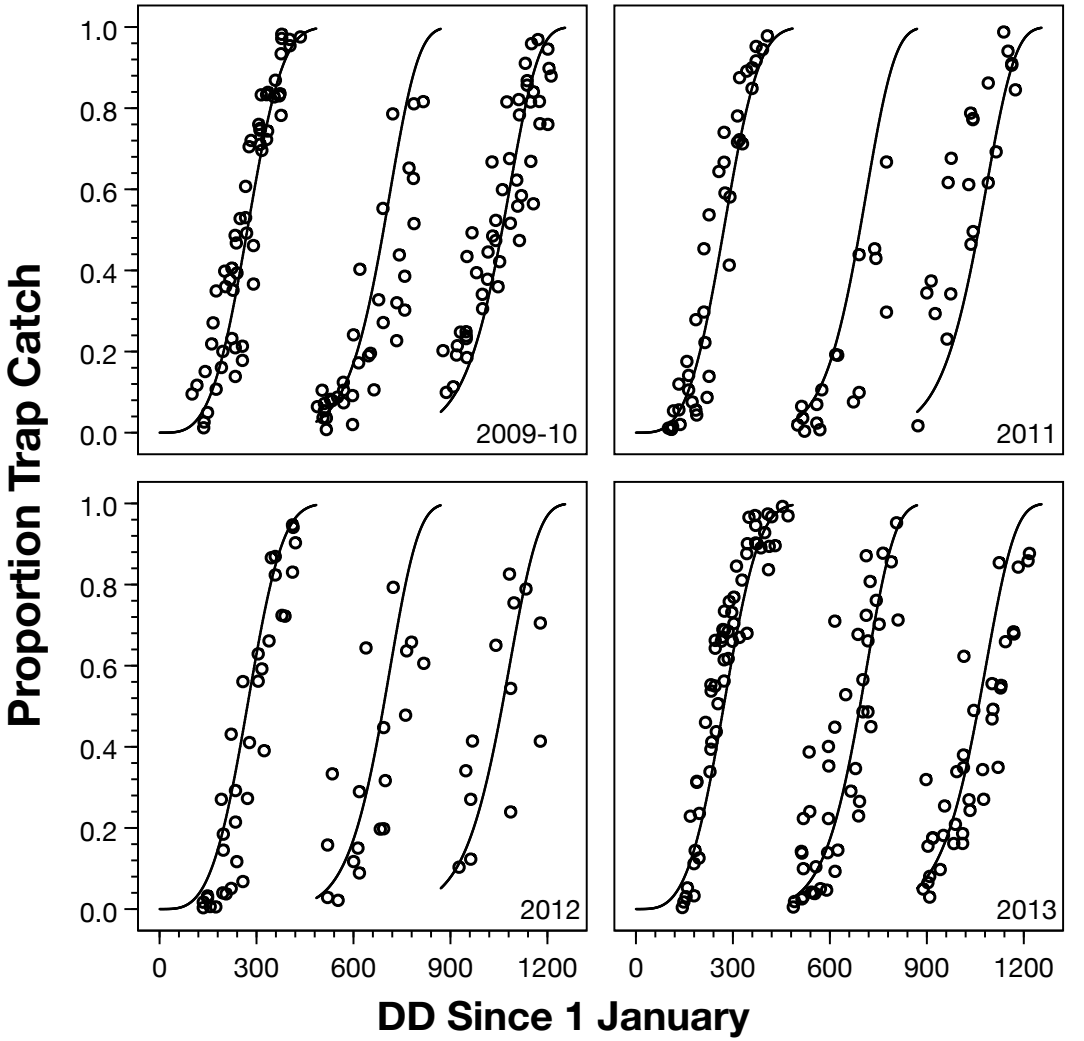
0.6
0.4
0.2
0.0
0
300
600
900
1200
DD Since 1 January

Figure2


Proportion Trap Catch
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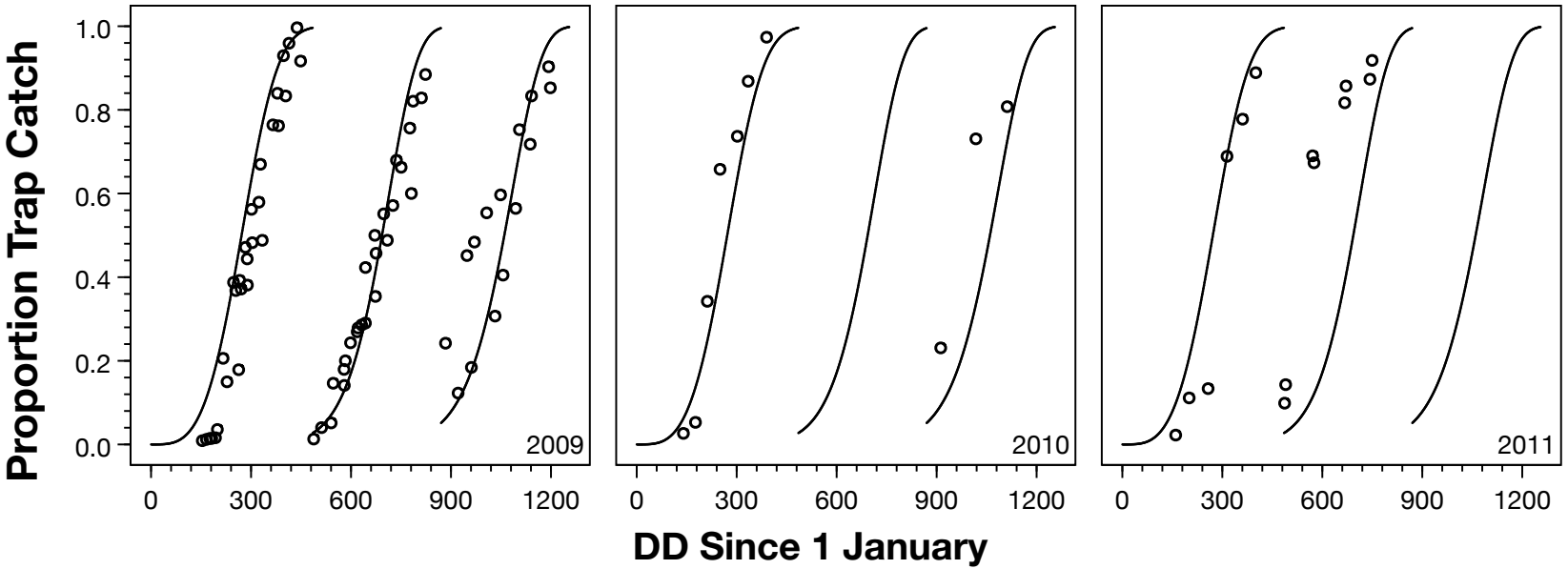
0.8
0.6
0.4
0.2
0.0
2009-10
2011
2012
2013
0
300
600
900
1200
DD Since 1 January

Figure3


Proportion Trap Catch
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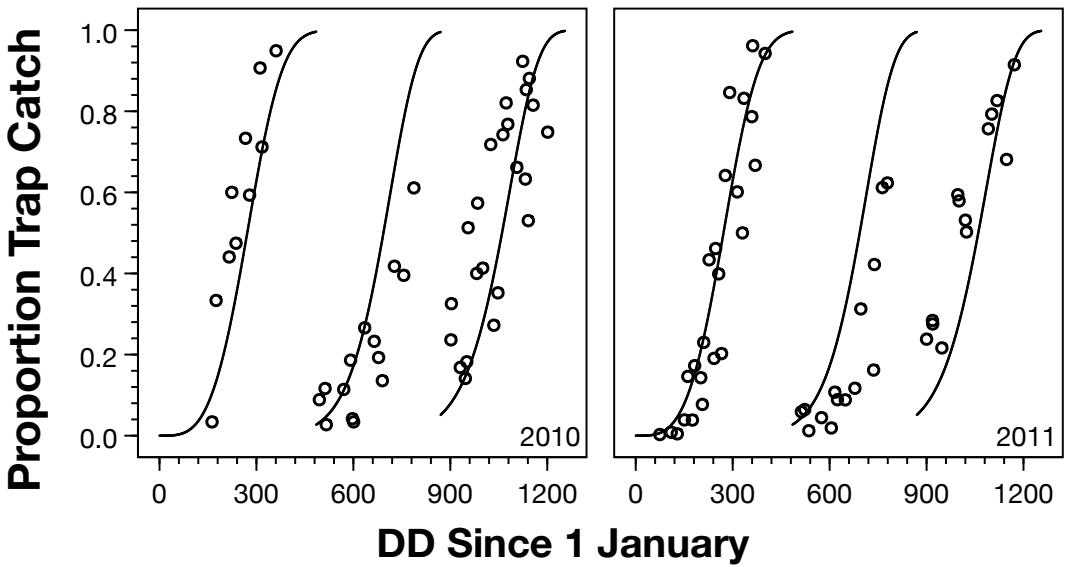
0.4
0.2
0.0
0
300
600
900
1200
2009
2010
2011
DD Since 1 January

Figure4


Proportion Trap Catch
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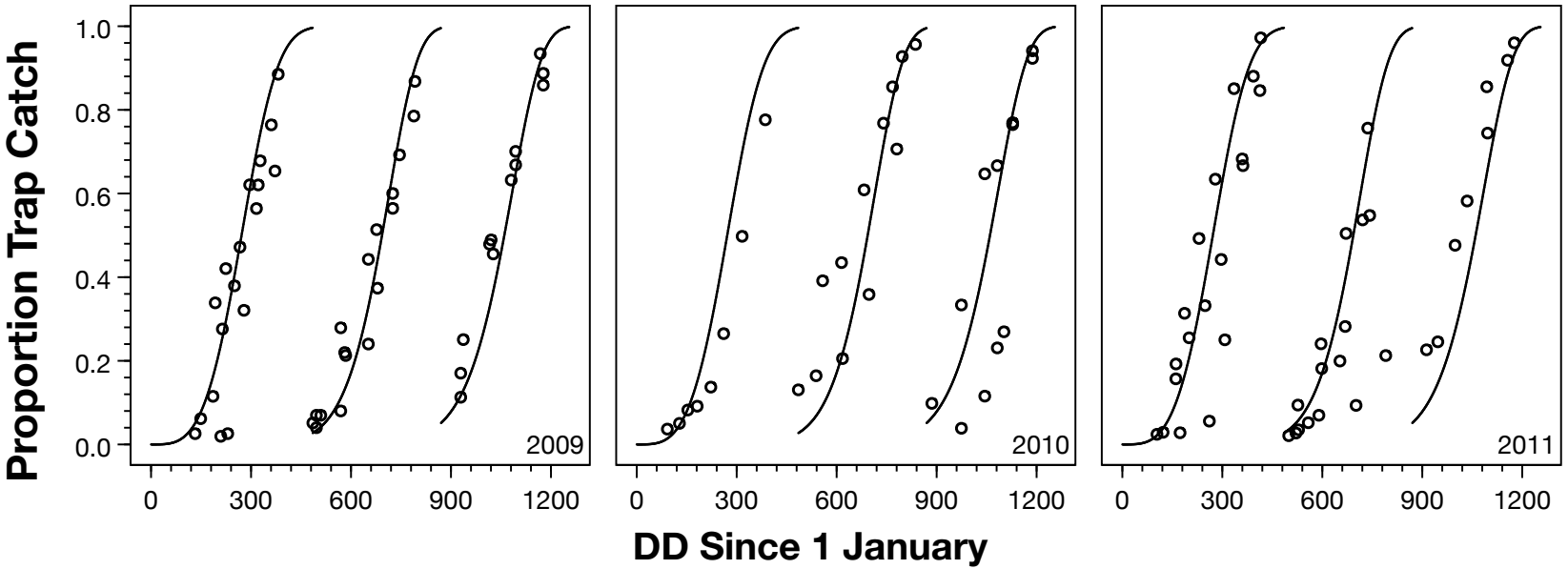
0.6
0.4
0.2
0.0
2010
2011
0
300
600
900
1200
DD Since 1 January

Figure5


Proportion Trap Catch
1.0
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0.6
0.4
0.2
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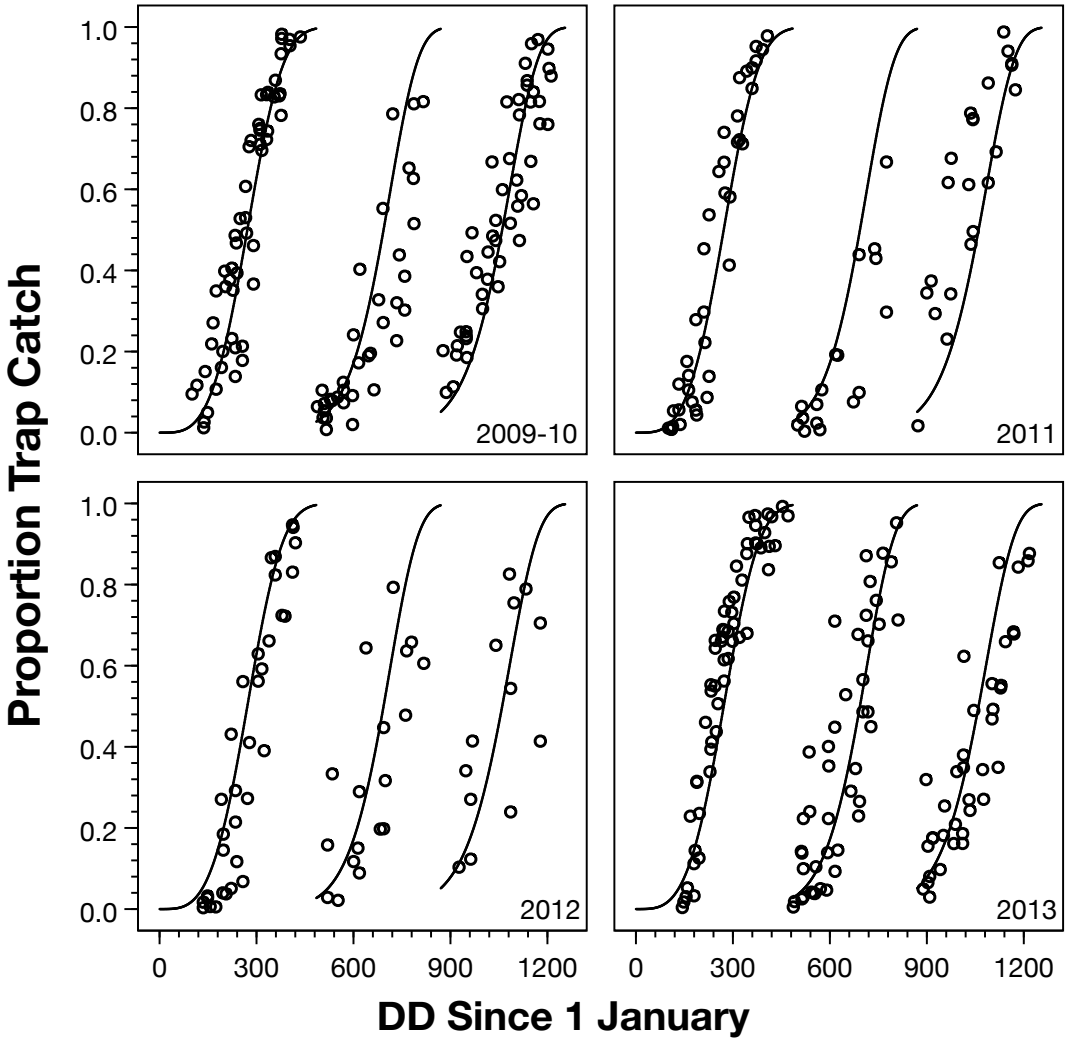
2009
2010
2011
DD Since 1 January

Graphical Abstract