Predictive Modelling of Adult Emergence in a Polyphagous *Eucolaspis* (Chrysomelidae: Eumolpinae) Leaf Beetle

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ABSTRACT *Eucolaspis* sp. "Hawke's Bay" (Chrysomelidae: Eumolpinae) is a pest that inflicts huge economic loss in many organic apple (*Malus domestica* Borkh.) orchards in New Zealand. The timing of control methods for this pest has been shown to be crucial for success. To aid in planning control programs, we studied threshold temperature and degree-days required for the development of *Eucolaspis* sp. "Hawke's Bay" pupae and modeled adult emergence in the field. Pupal development was observed at three constant temperatures. Pupae required 237.0 ± 21.67 degree-days above lower threshold temperature of 4.7°C ± 0.89°C to develop into adults. The emergence of adults was modeled with these thermal values and the model was tested for accuracy with field data. The model performed well with a precision of ±4 d. The proposed phenology model has wide applicability in monitoring and planning pest control measures.

KEY WORDS bronze beetle, Chrysomelidae, degree-day, phenology model, temperature

Eucolaspis Sharp 1886 (Coleoptera: Chrysomelidae: Eumolpinae), commonly referred as "bronze beetle," is a New Zealand native polyphagous leaf beetle genus. Recent taxonomic findings support only three mainland and one offshore species (Doddala 2012). One of these species, *Eucolaspis* sp. "Hawke's Bay" (Doddala 2012) is a pest on many economically important fruit crops in New Zealand. This species also infests other crops and native shrubs of the region. Damage by, *Eucolaspis* sp. "Hawke's Bay" results in loss of up to 40% of the yield in infested organic apple (*Malus domestica* Borkh.) orchards (Rogers et al. 2006). Limited options are currently available to organic growers for the control of this beetle.

All immature stages in *Eucolaspis* life cycle live exclusively underground, whereas adults live above ground (Miller 1926, Doddala et al. 2010). The larvae seem to undergo winter diapause in deep soil layers (450–600 mm) (Kay 1980, Rogers et al. 2008). Once soil temperatures are sufficiently high during late winter (August), larvae terminate their diapause and move upward, seeking food and shelter to pupate (Kay 1980). Thus, during spring (September and October), most larvae are found at a depth of <70 mm in the soil (Rogers et al. 2007, 2009). Pupation occurs in earthen cells in the upper soil layers during spring (Lysaght 1930, Rogers et al. 2006). So, this period provides a small window of opportunity for controlling bronze beetle immature stages when they are close to the ground surface.

Mechanical tillage of soil between apple trees in orchards exposes and destroys the larvae and pupae (Rogers et al. 2007). However, timing is critical for this control method, and cultivating too late in the season gave limited control of the beetle (Rogers et al. 2009). More recently, application of a bacterial formulation of *Yersinia entomophaga* has been shown to cause mortality of up to 40% of adult beetles (Hurst et al. 2011). In both cases, predicting accurately the developmental stage of the pest is important. Knowledge of insect phenology is crucial for the timing of pest management practices to target the most susceptible life stage of an insect pest (Delahaut 2003). Currently, there is very little information available on the phenology of *Eucolaspis.*

Insect development may depend on many environmental factors (e.g., temperature, photoperiod, humidity), although temperature is considered the most important (Howe 1967, Trudgill et al. 2005). Photoperiod may be crucial to certain biological events such as onset and termination of diapause, whereas humidity may limit distribution range (Regniere and Logan 2003). Temperature, however, seems to have a more direct effect on development of insects because as ectotherms, they are dependent on external (environmental) temperature for their thermal requirements (Delahaut 2003). Rates of development of ectotherms are slower at low temperatures than at high temperatures, and they accelerate within a specific range of tolerable temperatures (Jarosik et al. 2002, 2004; Trudgill et al. 2005). The base temperatures above and below which the development of an organism ceases (upper and lower threshold temperature, respectively) are usually species-specific, easy to measure under controlled conditions in the labora-

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Table 1. Parameters for calculation of thermal requirements for the emergence of *Eucolaspis* sp. "Hawke's Bay" adults from pupae, at three constant temperature regimes (12, 15, and 18°C) in the laboratory

T	n_p	n_a	N (±SE)	V	VT	V^2	T'	$(T - T')^2$	$(V - V')^2$
12	54	15	33.2 (0.9)	0.03	0.361	0.0009	11.88	0.01334	0.00015824
15	50	16	22.8 (0.6)	0.044	0.658	0.00192	15.27	0.07117	0.00000169
18	61	16	18.4 (0.7)	0.054	0.978	0.00295	17.85	0.02289	0.00013567
Σ			74.4	0.128	1.998	0.00578	45.00	0.10739	0.00029561

T is the experimental temperature; n_p is number of pupae monitored; n_a is number of adults emerged, N is the mean pupal duration; V is the mean developmental rate and equals $1/N$; VT, V^2, T', $(T - T')^2$, and $(V - V')^2$ are the other parameters used in calculation of threshold temperature and degree-days by using method 2 following Zong et al. (2004) and Ma et al. (2008); $V' = \Sigma V/n = 0.0428$; $n = 3$ is the number of temperature regimes in the experiment (12, 15, and 18°C); T' is the calculated value of temperature (or effective temperature) and equals $C_t + KV$.

tory, and effective in modeling phenology of target insects (Delahaut 2003, Jarosik et al. 2004, Trudgill et al. 2005). The other crucial parameter in phenology models, thermal constant, or the sum of effective temperatures (usually expressed in degree-days), is the total amount of heat required for an organism to develop from one stage to another in its life cycle (Honek and Kocourek 1990, Honek 1996) and has been used to predict phenology of insects and other ectotherms (Schwartz 2003).

Phenology models that predict seasonal occurrence of a particular growth stage are available for a range of coleopteran crop pests, including Western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Jackson and Elliott 1988, Stevenson et al. 2008); bark beetle, *Ips typographus* (L.) (Wermelinger and Seifert 1998); mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Logan and Powell 2004); *Semanotus bifasciatus* (Motschulsky) (Ma et al. 2008); bamboo powderpost beetle, *Dinoderus minutus* (F.) (Garcia and Morrell 2009); pine sawyer, *Monochamus galloprovincialis* (Olivier,1795) (Naves and de Sousa 2009); and brassica leaf beetle, *Phaedon brassicae* Baly (Wang et al. 2009).

To provide support for *Eucolaspis* sp. "Hawke's Bay" control programs, development of beetle pupae was studied in the laboratory. We used laboratory studies to assess lower threshold temperature and degree-days required for development of pupae into adults. The data were used to develop and test a phenology model for adult emergence in the field. Linear model was used to describe pupal development in bronze beetle, to calculate threshold temperatures, and to model adult emergence. Both linear and nonlinear models are in practice to describe insect development (Herrera et al. 2005). Nonlinear models enable description of insect development over a wide range of temperatures, but they may not be practically relevant (Jarosik et al. 2002). Linear models usually give a good fit for the rate of development over a range of ecologically relevant temperatures, and they are usually sufficient to predict insect development in the field (Campbell et al. 1974, Jarosik et al. 2002, Garcia and Morrell 2009). We believe that the linear model is appropriate here, as the temperature extremes near lower and upper developmental thresholds are unlikely to be experienced during the active growth period of *Eucolaspis* sp. "Hawke's Bay" in temperate New Zealand climate.

Materials and Methods

Insects and Incubators. Fully grown *Eucolaspis* sp. "Hawke's Bay" larvae that have terminated diapause and moved to the upper layer of the soil to pupate were collected during the last weeks of September 2009 and September 2010 from an organic apple orchard in Havelock North, New Zealand. Soil samples were taken below tree branches and hand-sorted (Rogers et al. 2006, Doddala et al. 2010). The larvae were collected individually into vented 1.5-ml microcentrifuge vials (Eppendorf AG, Hamburg, Germany) along with a small amount of soil. The larvae were kept cool and transported to the laboratory where they were maintained at controlled conditions (18°C, photoperiod of 0:24 [L:D] h) until they pupated. Care was taken that humidity did not fall below 80% by occasional water spraying and leaving water in open containers. The larvae were observed daily in the morning for pupation. Each new pupa was allocated randomly to one of three constant temperature treatments and transferred immediately to its respective incubator.

Three incubators were used for the experiment; each incubator was set at a constant temperature of 12, 15, or 18°C. These temperatures were within ±1°C of the mean monthly soil temperatures of the Hawke's Bay region during September, October, and November in the 3 yr (2006–2008) immediately preceding the year of experiment. Incubators were kept dark to simulate the conditions in soil where pupation occurs in nature. Humidity was not controlled but monitored with digital hygrometers. The vials were sprayed with distilled water if humidity fell below 80%. Temperatures were monitored using data loggers. The entire experiment was repeated in 2009 and 2010. Care was taken to have similar numbers of adults emerged from each temperature regime by adding more pupae depending on mortality in individual incubators (see Table 1 for details). The pupae were observed daily at noon for adult emergence. Adult status was accepted when the beetles achieved darker pigmentation (Lysaght 1930). Pupal duration was calculated as the number of days between the date of pupation and the date of adult emergence.

Calculation of Thermal Requirements. Lower threshold temperature and thermal constant (degree-days) required for *Eucolaspis* pupae to develop into adults were calculated based on two methods. For method 1 (Campbell et al. 1974, Naves and de Sousa 2009), rate of pupal development (y), the inverse of pupal duration (N) at a particular constant temperature, was regressed against temperature (T) as $y = a + bT$, where y is the rate of development, T is temperature in Celcius, a is the intercept, and b is the slope of the regression line. Rates of development of individual insects were used rather than the mean, in fitting regression model, to minimize error in estimation of thermal values (Kipyatkov and Lopatina 2010). The program Proc REG in SAS version 9.2 (SAS Institute, Cary, NC) was used for the regression analysis.

Threshold temperature, C_t, was calculated according to the formula $C_t = -a/b$, the temperature at which the regression line intercepts x-axis. The thermal constant, K, degree-days required, was calculated as the inverse of the slope of the regression line $K = 1/b$. Standard errors for threshold temperature (SE_{Ct}) and degree-days (SE_K) were calculated from the following formulae (Campbell et al. 1974, Walgama and Zalucki 2007):

$$S.E._{Ct} = \frac{y}{b}\sqrt{\frac{s^2}{n * y^2} + \left(\frac{S.E._b}{b}\right)^2}$$

$$S.E._K = \frac{S.E._b}{b}$$

where y is mean development rate, n is number of temperature regimes, s^2 is the residual mean square of y, b is slope of the regression line, and SE_b is the standard error of b.

For method 2, we followed Zong et al. (2004) and Ma et al. (2008). Thermal constant, K, threshold temperature, C_t, and their standard errors, SE_K and SE_{Ct}, respectively, were calculated using the following formulae:

$$K = \frac{n\Sigma VT - \Sigma V \Sigma T}{n\Sigma V^2 - (\Sigma V)^2}$$

$$S.E._K = \sqrt{\frac{\Sigma(T - T')^2}{(n-2)\Sigma(V - V')^2}}$$

$$C_t = \frac{\Sigma V^2 \Sigma T - \Sigma V \Sigma VT}{n\Sigma V^2 - (\Sigma V)^2}$$

$$S.E._{Ct} = \sqrt{\frac{\Sigma(T - T')^2\left[\frac{1}{n} + \frac{V'^2}{\Sigma(V - V')^2}\right]}{n-2}}$$

where n is the number of temperature regimes in the experiment, T is the experimental temperature, N is the mean number of development days (i.e., pupal duration), and V is the mean developmental rate and equals $1/N$, $V' = \Sigma V/n$ and $T' = C_t = KV$.

Weather Data. Weather data on daily mean soil temperature (at 10-cm depth) in Hawke's Bay were retrieved for 2005–2007 and 2009 from an online database (Pipfruit NZ 2012) and used in model testing.

Development and Evaluation of Phenology Model. A phenology model that predicts date of adult emergence was devised as biofix date + N, with the thermal values obtained through laboratory studies and weather data as inputs, where N is the pupal duration that is equal to i when $\Sigma_1^i(T_i - C_t) \geq K$, T_i is the mean soil temperature at 10-cm depth (in Celcius) on ith day, C_t is the lower threshold temperature (in Celcius), and K is the degree-days required (Celcius days). The rectangular method (without any upper cutoff) was used to calculate daily effective temperatures and accumulate degree-days (Wilson and Barnett 1983).

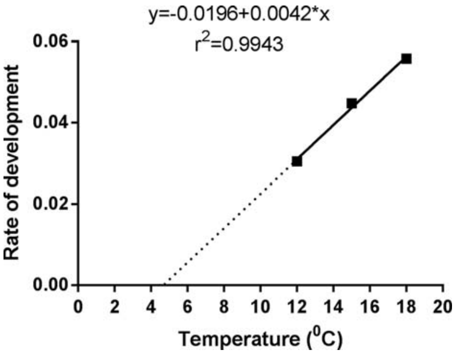

Fig. 1. Relationship between temperature and the rate of development in *Eucolaspis* sp. "Hawke's Bay" pupae in the laboratory; rate of development is equal to inverse of pupal duration at a given temperature.

A biofix date is an arbitrary date of the start of a developmental stage (in this case, day 1 of pupation). Because the start date of pupation in the field was not recorded and could not be estimated accurately, we tested four dates (1, 6, 11, and 16 September) at 5-d intervals spanning the likely period in September when we estimate beetle pupation begins. The model thus predicts emergence with an accuracy of ±4 d and is within the normally accepted 10–15% error (Higley et al. 1986, Naves and de Sousa 2009). Testing different biofix dates in the absence of an empirical date is well supported by published literature (Umble and Fisher 2000, Naves and de Sousa 2009).

Predicted emergence dates (date of first adult beetle emergence) were generated for 2005, 2006, 2007, and 2009 by using different biofix dates and compared with actual emergence dates in those years obtained from the emergence monitoring data in the Hawke's Bay orchards (Rogers et al. 2006, 2007; Doddala 2012; D.J.R., unpublished data). Absolute differences between predicted and actual emergence dates were calculated, and the best biofix date that produced least absolute deviation from actual date is used for further analysis.

Results

In the laboratory bioassays, the rate of development of pupae increased as the temperature increased from 12 to 18°C, with a strong linear relationship ($P < 0.001$) (Fig. 1). It took an average of 33.2, 22.8, and 18.4 d for *Eucolaspis* sp. "Hawke's Bay" pupae to develop into adults at constant temperatures 12, 15, and 18°C, re-

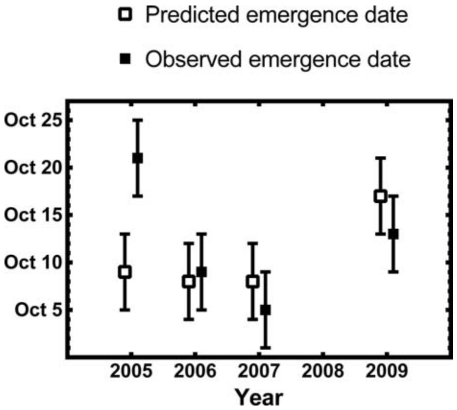

Fig. 2. Predicted (±4 d) and observed (±4 d) dates of first emergence for adult *Eucolaspis* sp. "Hawke's Bay" beetles in organic apple orchards in Hawke's Bay, New Zealand, in different years.

spectively (Table 1). The sex of emerging adults was not recorded.

Threshold Temperature and Degree-Days Required. Lower threshold temperature for development of *Eucolaspis* sp. "Hawke's Bay" pupae was found to be 4.7 ± 0.89°C, when calculated using method 1 as (x; 0) intercept of the regression line in the Fig. 1. The threshold temperature was 4.5 ± 0.84°C when calculated using method 2 (using parameters in Table 1).

Degree-days (Celcius days) required for completion of pupal development were equal to the inverse of the slope of the regression line (Fig. 1) and were 237.0 ± 21.67 according to method 1 and 246.2 ± 19.06 according to method 2 (using parameters in Table 1).

Phenology Model. Lower threshold temperature and degree-days calculated using the two methods did not differ greatly; 4.7°C and 237 degree-days obtained from the more widely referenced method 1 (linear regression model) were used to predict adult beetle emergence.

Among the different biofix dates compared for the accuracy of prediction, 11 September gave the best fit model with the least mean absolute deviation (5 d) between predicted and actual emergences, compared with the other dates tested (1 September, 9.25 d; 6 September, 6.5 d; 16 September, 7.5 d).

The predicted and actual emergence dates when 11 September was used as the biofix date were within ±4 d for all the years except for 2005, where the difference between the two dates was >10 d (Fig. 2). Among the investigated years, 2006 and 2007 had the earliest predicted emergence date due to high soil temperatures, and 2009 had the latest predicted emergence date due to low soil temperatures.

Discussion

As found in the current study (Fig. 1), increased rate of development at higher temperatures also was observed in eggs of *Eucolaspis* by Lysaght (1930), who observed that eggs hatched after 21–22 d during early in the season (late spring), whereas they hatched in only 15 d later in summer, when temperatures were higher. Acceleration of development with increase in temperature within an optimal range is typical of ectotherms (Jarosik et al. 2002, 2004; Trudgill et al. 2005).

Developmental thermal values (threshold temperatures and degree-days) are usually taxon-specific, and they represent the evolutionary adaptations of an organism to its thermal environment (Trudgill et al. 2005). We believe that the 4.7°C lower threshold temperature calculated for *Eucolaspis* sp. "Hawke's Bay", which temperature seems to be much lower than the observed average for Coleoptera (13.6°C) (Nietschke et al. 2007), is an ecological adaption to New Zealand's temperate climate. Similar lower threshold temperatures for pupal development (<5°C) were observed in other coleopterans, such as strawberry root weevil, *Otiorhynchus ovatus* (L.) (Coleoptera: Curculionidae) (4.3°C) (Umble and Fisher 2000); and bamboo powderpost beetle (Coleoptera: Bostrichidae) (4.5°C) (Garcia and Morrell 2009).

The accuracy of thermal constants calculated from linear models as used in the current study depends on the ecological relevance of the experimental temperatures, i.e., the experimental temperatures should be representative of the environmental temperatures during the organism's active developmental period (Bergant and Trdan 2006). Accordingly, our experimental temperatures represent the most probable range of temperatures in the field during active pupal growth, i.e., September–November (Lysaght 1930, Rogers et al. 2008).

A particular strength of the proposed phenology model for *Eucolaspis* sp. "Hawke's Bay" is that is has been validated with the field data. The model was effective in estimating the emergence of adult beetles in the field. Among the four biofix dates tested, 11 September (11th day after the start of New Zealand meteorological spring in a year; 254th day in a 365-d year) was most accurate in predicting the date of first emergence (Fig. 2). The first pupal appearance in the field was not usually observed before the first week of September each year (D.J.R., unpublished data), providing further support for the chosen biofix date. When 11 September was used as the biofix date, all predicted emergence dates (with the exception of 2005) of the bronze beetle adults fell within ±4 d (mean deviation, 9.5%) of the observed emergence dates in organic apple orchards of Hawke's Bay. Usually, predictions that are within 10–15% of the actual dates are considered adequate (Higley et al. 1986, Naves and de Sousa 2009). The larger discrepancy between predicted and observed date of beetle emergence in 2005 may be an artifact of a late start of field monitoring of adult bronze beetles in 2005, when the beetles that emerged before 21 October may have been missed (Rogers et al. 2006).

The emergence of bronze beetle adults in the field typically continues for ≈8 wk, and ≈80% of the beetles emerge during November (Rogers et al. 2007). More than 50% of the adults had emerged by the second week of November each year (except in 2007, 36%

Table 2. Dates of observed emergence in the field and corresponding predicted dates of pupation for *Eucolaspis* sp. "Hawke's Bay" populations in organic apple orchards in Hawke's Bay, New Zealand (2005–2007 and 2009)

Yr	Pupation		Emergence	
	50%	90%	50%	90%
2005	24 Oct.	14 Nov.	12 Nov.	3 Dec.
2006	15 Oct.	12 Nov.	6 Nov.	27 Nov.
2007	6 Nov.	24 Nov.	23 Nov.	7 Dec.
2009	17 Oct.	15 Nov.	13 Nov.	4 Dec.

emergence) and 90% of the adults had emerged by the first week of December (Table 2). If these crucial events (50 and 90% emergence) were back-calculated in time in the bronze beetle life cycle, by using the phenology model proposed here and weather data for 2005–2007 and 2009, it seems that 90% pupation of the bronze beetle would be reached by the second week of November (except in 2007). These pupation dates (Table 2) suggest that control methods such as cultivation should be executed before the third week of October to be most effective, as most of the beetle population will be at either pupal or late-instar larval stages and thus vulnerable to the disturbance of the soil.

Other applications for the suggested phenology model include predicting emergence of beetles in the orchards from historic weather data. With biofix date of 11 September and historic mean soil temperature data for 30-yr period 1971–2000 (NIWA 2011a), the predicted first appearance of adult bronze beetles in Hawke's Bay apple orchards would be on 15 October. The biofix date recommended here (11 September) gave accurate predictions for three of the 4 yr considered, and so the model can be used successfully as it is. Indeed, our pheonology model was effectively used during 2012 to predict adult emergence in Hawke's Bay with precise results (D.J.R., unpublished data). Fine-scale utility of our model can be enhanced by the inclusion of location specific pupation time. Individual orchardists can identify the date of first pupation by monitoring larvae and pupae in the orchard soil during a few weeks from late August. The phenology model can then be used to accurately predict the start of beetle emergence in that particular orchard, by replacing the biofix date with the date of first pupal appearance and using local weather forecast for accumulating degree-days.

Studying thermal regulation of diapause and thermal requirements of postdiapause prepupal larval instar(s) could enhance robustness of our phenology model. There is no information currently available about which larval stage(s) in *Eucolaspis* sp. "Hawke's Bay" would undergo diapause. However, if it is shown that only one larval instar undergoes the diapause, and accurate diapause termination data are available, thermal requirements of the diapausing instar could be estimated. This estimation would provide more predictive accuracy for the timing of pupation and thus would fine tune the model. Studying thermal biology of other immature stages of *Eucolaspis* sp. "Hawke's Bay" would enable prediction of outbreaks, expansion to new geographic areas and future challenges influenced by changing climate. Currently, the geographic distribution of *Eucolaspis* sp. "Hawke's Bay" in New Zealand seems to be dictated by temperature distribution. By 2040, annual temperatures across all regions of New Zealand are predicted to increase by up to 1.3°C (NIWA 2011b). This increase might have important implications for apple orchards in southern regions of New Zealand (e.g., Central Otago), where bronze beetle has not yet established.

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