ORIGINAL CONTRIBUTION

Development and validation of a phenological model for the univoltine European corn borer

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Abstract

Biological control of a univoltine race of European corn borer, *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae), by *Trichogramma* in Switzerland is currently timed according to repeated, semi-field observations of the post-diapause development of the pest at one site. We developed a phenology model with the aims of replacing this costly labour practice and by considering the Swiss landscape. Observations collected over 29 years were used for model calibration and validation. We parameterized a time-varying distributed delay model based on published laboratory observations of development durations at constant temperatures. The model was driven with hourly temperature recordings beginning on January 1. The calibration of the mean development rates and their variations was based on semi-field data of larval and pupal development. The model, with its calibrated parameters and their variations, allowed the simulation of mean predictions and prediction intervals. We validated the model predictions of emergence with flight data (obtained via light traps) from several sites in western and northern Switzerland. The simulated mean emergence was 6.9 degree-days earlier than the observed flight at the calibration sites and only 0.5 degree-days earlier than the observed flight at other sites. Our simulation of pupation explained half of the variation in emergence time, whereas semi-field observations of pupation explained three-quarters of this variation. Our model simulations are not subjected to the local potential biases. Simulation errors from a year with an extremely dry spring were explained by the lack of consideration of humidity by the model. Our simulations provide a valid and less labour-intensive alternative to observations for timing biological control in the maize-growing areas of Switzerland and likely other areas of Europe.

Introduction

The European corn borer (ECB), *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae), is a major pest in all maize-growing areas of the world. The known races are defined according to their pheromone (Z or E) and their generation number (uni-, bi- or multivoltine) (Showers et al. 1978; Glover et al. 1987; Linn et al. 1997; Marçon et al. 1999). In southern Europe, Z- and E-pheromones have been reported, as

have two and three overlapping generations, whereas in central Europe, only the Z-pheromone and one generation was present until recently (Derron and Goy 2006). In southern Germany, a bivoltine population has appeared only in recent years (Pölitz et al. 2007; Albert et al. 2008). In northern Switzerland in the 1970s, ECB was only a local agricultural problem, but later, ECB spread to all maize-growing areas of Switzerland (Bigler and Bosshart 1992; Derron and Goy 2006). During the first years after detection in

Switzerland, univoltine populations were observed north of the Alps, with bivoltine populations observed south of the Alps. Since the turn of the century, bivoltine populations have also been found in the Lake Geneva Basin of Switzerland (Derron et al. 2009). E-pheromones were never reported north of the Alps.

Control of the univoltine ECB race (1ECB) in Switzerland is based on releases of *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae), an oophagous parasitoid. It is the only permitted plant protection measure against 1ECB and is applied over a large area. Biological control of the bivoltine race, or mixed populations, is more challenging and not often practiced. For synthetic insecticide use, specific authorization of cantonal phytosanitary services is required.

Univoltine and bivoltine ECBs overwinter as diapausing L5 larvae in above-ground corn plant debris. After diapause, larvae resume development in the spring and pupae are found in June. Moths emerge and females lay eggs from mid-June until mid-July. Larvae feed on stalks during the summer until the end of August, when diapause begins. Synchronization between parasitoid emergence and 1ECB oviposition is crucial for successful biological control (Hawlitzky 1986; Smith 1996). To best control 1ECB eggs, parasitoids must be released at the beginning of 1ECB flight, near the end of June.

The most direct manner to time parasitoid release is to observe 1ECB phenology. This approach is applied by Agroscope (Swiss centre for agricultural research) at one site at Changins in western Switzerland, and the results are used to time parasitoid releases for all of Switzerland (Derron and Goy 2006). Current predictions of flight used for timing parasitoid releases are based on the following information:

1 Beginning of pupation, based on daily observations of 1ECB individuals in maize stalks.
2 Amount of lag between pupation and flight, based on historical observations (Derron and Goy 2006) during the years 1985–2004.

After the alert of Agroscope of the expected beginning of flight, rearing companies initiate parasitoid preparation to ship parasitoids for release by maize producers. Currently, Agroscope offers this service free of charge but is looking for an alternative to reduce the expenses. Modelling can circumvent cumbersome observations of 1ECB development (Losey et al. 1995) and is not restricted to a specific site. In Switzerland, two models have been developed using a descriptive approach to fit field

observations (Derron and Roth 1986; Derron and Goy 2006). In the present work, we chose to use a mechanistic approach because it has the advantage that parameters contain biological meaning; thus, adaptations to a change in biology are easier to implement.

Insect phenology has been modelled using various mechanistic approaches, and several models have been applied to predict ECB flight (Anderson et al. 1982; Brown 1982; Kelker et al. 1990; Magai et al. 1997; Trnka et al. 2007; Maiorano 2011). Flight phenology is mainly influenced by voltinism (McLeod 1976; Derron et al. 2009). The first generation of bivoltine populations flies earlier than the first generation of univoltine populations. Got et al. (1996) developed a phenological model for pre-diapause ECB larvae in France. As with the majority of insects in temperate regions, temperature is the main factor driving 1ECB development (Jarvis and Brindley 1965; McLeod 1981; DuRant 1990), and the influence of temperature can be described by several functions (Farooqi and AliNiazee 1997). A linear relationship has the advantage of simplicity and validity in most cases (Matteson and Decker 1965; Kelker et al. 1990). The variability in development has also been represented using different approaches (Gilbert et al. 2004; Yurk and Powell 2010). The distributed delay approach (Manetsch 1976; Plant and Wilson 1986) was previously implemented in our modelling environment with satisfaction (Graf et al. 1996; Schaub et al. 2005; Samietz et al. 2007).

The published ECB models were not parameterized with European insects and were primarily validated under North American conditions or with multivoltine populations (Maiorano 2011). A validated mechanistic phenological model of 1ECB for estimating the timing of parasitoid release related to 1ECB flight in Europe is missing.

Our study aimed to parameterize, calibrate and validate such a model. We acquired parameters from published laboratory experiments (Derron et al. 2009). We calibrated and validated our model using original data sets by Derron and Goy (2006) that were supplemented with our data from the subsequent year. The results are a 29-year observation series of larval and pupal development in semi-field conditions (an insectary) and of flight in field conditions (maize fields) from several regions in Switzerland. We divided the observation series according to conditions, years and sites for several purposes:

A Calibration

  1 Comparison of simulations using original parameters with semi-field observations of larval and pupal development (CAL1);
  2 Re-adjustment of parameters to better match the same observations (CAL2);

B Validation

  1 Comparison of simulations with other, partially independent, semi-field observations of larval and pupal development (VAL1);
  2 Comparison of simulations with completely independent field observations of flight at Changins (VAL2);
  3 Comparison of simulations with completely independent field observations of flight at sites other than Changins (VAL3); and
  4 Comparison of simulations with observations of pupation used to predict flight observations (VAL4). The motivation is to compare our simulations with current practices of timing parasitoid releases.

Materials and Methods

Model structure and parameters

The model simulates the development of 1ECB from diapause termination to the emergence of adult moths (Graf et al. 1996). Post-diapause development begins after diapause and ends with pupation, whereas pupal development ends with the emergence of adults. The simulation was initialized on January 1 and its time step was one hour of the Julian date time scale (JD).

If the temperature (T) exceeds the thermal threshold (τ), the development rate (r) is linearly dependent on temperature, while γ represents the thermal constant (Huffaker and Rabb 1984; Kelker et al. 1990):

$$r = \frac{1}{\gamma} * (T - \tau)$$

The term ($T-\tau$) multiplied by time is the physiological time or named here 'degree-days' (DD) and the unit is centigrade-days.

A time-varying distributed delay approach (Manetsch 1976) was used to simulate post-diapause and pupal development assuming zero mortality. The outcome of this method is to represent the variability of individual transit times through the development stage with an Erlang frequency distribution. The shape parameter of this κ distribution depends on γ and its standard deviation (s):

$$\kappa = \frac{\gamma^2}{s^2}$$

The results of simulations are cumulative density functions of all life stages depending on time. Representations of cumulative density curves were simplified by logit transformation. Two values best characterizing simulations were calculated by linear regression for every available year (fig. 1):

1 Mean duration to reach 50% cumulative density (JD50 or DD50).
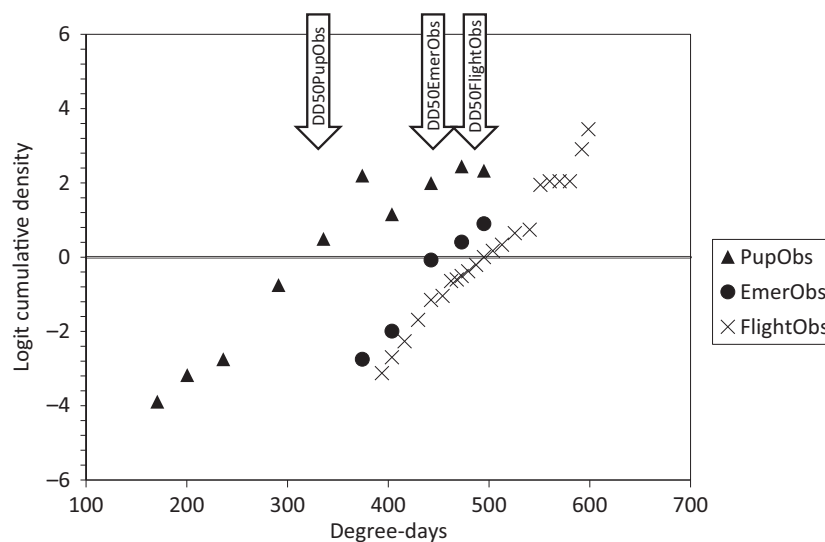2 Slope of the cumulative density function (JDSL or DDSL).

Fig. 1 Data set for a typical year (2000): Observed pupation, emergence and flight vs. degree-days (DD). DD50: mean observed degree-days (DD from January 1 until 50% cumulative density).

The first value expresses the mean duration from January 1 to reach a given stage, and the slope is a measure of the variability of this duration.

Parameterization

Original values of the parameters (table 1) were extracted from laboratory observations of development rates at one temperature and from the known thermal threshold. Two points are sufficient to define the linear rate–temperature relationship. The first point is the generally accepted thermal threshold (τ) of 10°C in America and Europe (Apple 1952; Jarvis and Brindley 1965; Kelker et al. 1990; Trnka et al. 2007). The second point is based on Derron et al. (2009) observations of post-diapause and pupal development of 539 and 225 individuals, respectively, of 1ECB in the laboratory at 20°C between 1982 and 1984. The authors assured diapause by storage at 4°C for 150 days and did not report mortality. The values of γ and s were estimated with the inverses of the rate values.

Observations

The timing of 1ECB pupation and emergence in Switzerland were observed at Changins from 1985 to 2013, whereas flight observations were available only until 2000 (figs 1 and 2). Flight was also observed at additional sites in Switzerland over several years (table 2): Geneva (1981–1987), Chablais (1982–1983) and Aarau (2012–2013). These sites are approximately 30, 100 and 180 km away from Changins, respectively. Available observational data sets were separated and assigned according to purpose (CAL1–CAL2, VAL1, VAL2, VAL3, VAL4, fig. 2). Pupation and emergence observations consisted of counting new pupae or pupal exuviae in semi-field conditions, while flight observations were based on trap captures in the field. All observations were acquired by the same Agroscope laboratory, and the observations made until 2004 were published by Derron and Goy (2006).

Table 1 Original (Derron et al. 2009) and calibrated thermal constants (γ) and standard deviations (s) of post-diapause and pupal development (in degree-days)

Stage	Original		Calibrated	
	γ	s	γ	s
Post-diapause	330	85.1	310.7	75.6
Pupae	179	19.2	173.9	17.0

1ECB-infested stalks were collected during the previous autumn in one field of each region where bivoltine ECB were not known to be present. During the winter, approximately 400 stalks were stored in semi-field conditions outdoors in four crates placed on the soil at Changins, imitating maize field conditions. During 1985–2008, in the spring and twice per week, sufficient stalks were removed from the crates and opened to obtain 50 individuals, and the individual developmental stages were identified as larvae, pupae or pupal exuviae. In 1998–2013, at least 100 larvae were isolated from the stalks and transferred to rearing boxes stored in the insectary under ambient temperatures. In these boxes, pupae and pupal exuviae were counted every day. Examination included estimation of mortality in the boxes but not in the stalks. Mortality in the boxes was 9% for larvae and 23% for pupae. The stalks in the crates were exposed to wind and rain, and the content of the boxes was humidified every other day.

Flight in field conditions was observed daily from March until November in regions where bivoltine ECB were unknown. Light traps attracted adults with incandescent bulbs, accumulated them with a funnel and killed them in a gas chamber containing an anaesthetic liquid (Hächler 1989; Derron and Goy 2006). Traps were checked and emptied daily.

The time of an observation is defined as the midpoint between the date of the observation and that of the previous observation. The first and last observations of a time series were considered too unreliable and insignificant for inclusion in the data analysis. Therefore, only observations between cumulative density values of 0.01 and 0.99 were considered. To characterize observations with two values, DD50 or JD50 values, as well as DDSL or JDSL values, were calculated after logit transformation as described above.

Driving variable

The hourly ambient temperature data at 2 m height measured by the automatic weather stations closest to the observations sites were acquired from the MeteoSwiss (www.meteosuisse.admin.ch) national weather service (table 2). The weather stations and light traps were situated at elevations between 380 and 460 m above sea level.

At Changins, where the observations for calibration and validation were acquired, the distance between the weather station and the observation site was <20 m.

Fig. 2 Mean observed degree-days from January 1 (DD50) to pupation, emergence and flight (pup, emer and flight, respectively) for all years at Changins. Observations were collected via different methods (crate, box or trap) for calibration (CAL1, CAL2 with semi-field observations) and validation (VAL1 with semi-field observations, VAL2 with field observations, VAL3 with semi-field and field observations).
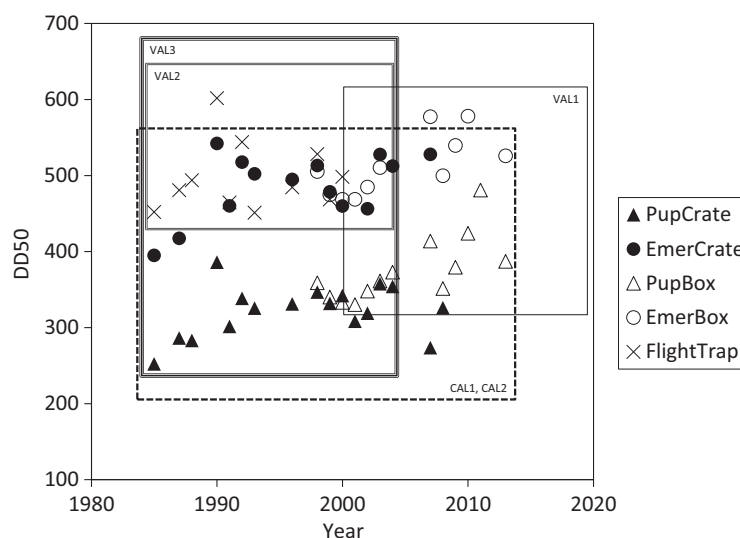
Table 2 Numbers of observational data sets acquired using various methods and the weather stations for the observation sites

| | No. of years | | | |
| | Pupation and emergence (semi-field) | | Flight (field) | |
Site	Crate	Box	Trap	Weather station
Changins	18	13	11	Nyon/Changins VD
Genève			6	Genève-Cointrin GE
Chablais			3	Aigle VD
Aargau			2	Buchs AG

Calibration

For the calibration of CAL1–CAL2 of parameters, simulations using the original parameters were compared with semi-field observations of pupation and emergence in crates at Changins (fig. 2). Parameters for post-diapause and pupal development were adjusted to match the simulation results to the corresponding observational data. The thermal constant (γ) values were calibrated by dividing them by the mean yearly proportional error (π) values, that is simulated/observed DD50 values, or bias. The shape parameter (κ) values were calibrated by manual iteration to equalize the means of the simulated and observed yearly DDSL slope values.

The standard deviation (σ) of π was used to estimate the prediction intervals of the simulations, with a given probability. Prediction intervals describe distributions of future values rather than uncertainties in the estimations of population means, as do confidence intervals. The limits of the prediction intervals were defined by dividing γ by $\pi - z*\sigma$ and $\pi + z*\sigma$, where z is the quantile of the standard normal distribution (P = 0.95; z = 1.96).

Validation

For VAL1 validation, simulations were compared with semi-field observations of pupation and emergence collected for boxes at Changins (fig. 2). In five of 11 years, the observed individuals were the same individuals as those observed in crates during the calibration. For VAL2 validation, emergence simulations were compared with field observations of flight at Changins and other sites. VAL1 and VAL2 validation was assessed by comparing simulated and observed DD50 and DDSL values of pupation and emergence. A comparison was performed by calculating the proportional deviation and paired t-tests.

The VAL3 validation consisted of comparing the simulated results and semi-field observed data regarding the time between pupation and flight in the field at Changins (fig. 2). The observed flight JD50 values were regressed on JD50 values of simulated and observed pupation. The coefficients of determination (r^2) represent the proportion of total variation explained by regression.

Results and Discussion

Calibration

To improve the simulations of developmental duration, the thermal constant (γ) values of pupal and

larval stages were reduced (CAL2, table 1, fig. 3). This calibration corrects for unknown, systematic sources of errors in temperature measurements and thresholds.

With calibration, the biases (π) of γ of the post-diapause (P = 0.543) and pupal (P = 0.883) developmental stages were negligible, but the random errors were considerable. The slopes of the cumulative density functions (fig. 4) represent the individual variations within each year, and the prediction intervals estimate the variations of these functions between years. These intervals describe unknown causes of interannual variability associated with modelling insect biology and with calibration observations.

Not surprisingly, the durations in degree-days required to reach pupation and emergence were similar to those reported by Derron and Goy (2006) for

1985–2004 because both values were based primarily on the same data. For example, Derron and Goy (2006) observed 5% pupation at 192 DD and a lag of 5% emergence of 168 DD, while our simulations produced 5% pupation on average at 199.9 ± 2.8 DD and a lag of 167.6 ± 5.0 DD. These differences are mainly attributable to the differences between the temperature summation methods. This study used hourly data and integration, whereas Derron and Goy (2006) used daily min–max data and daily mean integration.

The simulated slope of pupation was raised by increasing the parameter for post-diapause development, causing a decrease in the standard deviation (s) of the thermal constant (CAL2, fig. 3). The parameter κ for pupal development could not be adjusted because the emergence slope also depends on post-
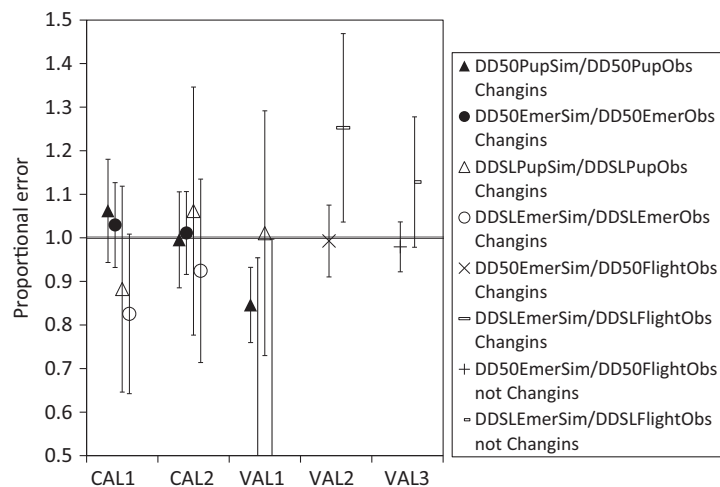

Fig. 3 Mean proportional error (π ± standard deviation) of all years between the simulated and observed mean degree-days (DD50) and slope values (DDSL) for calibration (CAL1 before, CAL2 after; with semi-field observations) and validation (VAL1 with semi-field observations, VAL2 with field observations, VAL3 with semi-field and field observations).
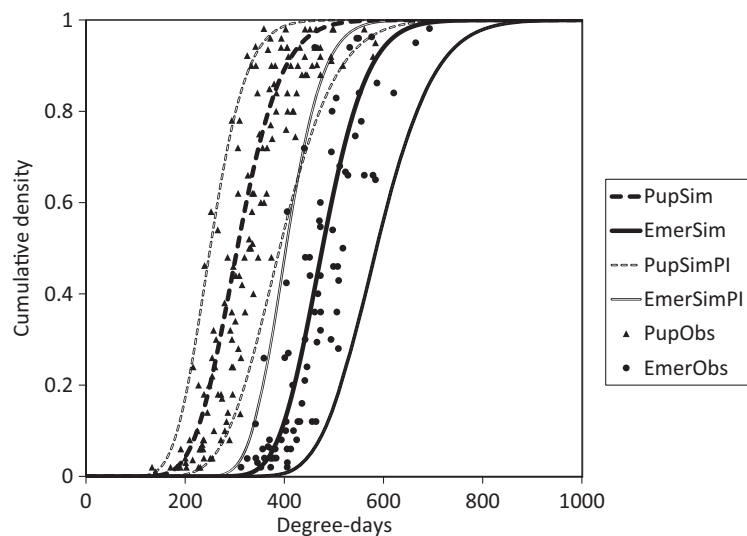

Fig. 4 Cumulative density of pupation and emergence vs. degree-days from January 1 (DD): Mean prediction and prediction interval (PI, P = 0.95) of the calibrated model (CAL2) and observations used for the calibration for all years at Changins.

diapause development. The calibration of pupal development was set as equal to post-diapause development.

All observations used in this study were obtained with the aim of practical flight prediction and not model development. Therefore, with respect to the present aim, the available observation data suffered from some methodological limitations. During the 29 years of observations at Changins, the observational method (crate vs. box) and the sites of the stalk crates were altered. Analysis of the observations from years in which both observational methods (1998–2004) were applied did not suggest that this change in environment affected larval or pupal development. The growth of vegetation at the site and the relocation of crates in 2007 from the middle of a lawn to the border of an adjacent parking lot may have influenced the microclimate. These various influences may be the cause of the increases in degree-days for pupation and emergence observed during the long observation period (fig. 2).

Validation

During VAL1 validation, simulated emergence was 26.0 DD earlier (P = 0.043) than observed emergence, and simulated pupation was 61.2 DD earlier than observed (P < 0.0001) (fig. 3). Biases were caused by an increasing number of degree-days measured by MeteoSwiss that were required to reach pupation and emergence during the course of the study (fig. 2).

The fit of the validation data for emergence physiological time was excellent. At Changins, the simulation emergence was an average of 6.9 DD early (VAL2, P = 0.618, fig. 3), and at all other sites, simulated emergence was only 0.5 DD early (VAL3, P = 0.210).

The slopes of the cumulative density function were not well simulated in the validation for Changins (VAL2, P = 0.003) or for the other sites (VAL3, P = 0.019). The simulated emergence slopes were steeper than the flight slopes. The increased variability in duration of flight was probably caused by the increased complexity (behaviour, mortality) in the field compared with the simulated development in semi-field situations.

During VAL4 validation, the regression of the date of 1ECB flight on observed pupation date performed better than the regression of the date of 1ECB flight on simulated pupation date (fig. 5). Our simulations explained 47% of the variation in flight date, whereas the observations explained 72% of the variation. This difference is mainly attributed to year 1990. Not considering this year, the simulation and observation explained the same variability (73%, 71%). In 1990, flight, pupation and emergence were exceptionally late (fig. 2). The temperatures during this year and the ones of the fall of the previous year were not extraordinary. March of 1990 was very dry with only 8.1 mm precipitation during 33 days. Prolonged (30-day) exposure to dry conditions and long day lengths hampers diapause termination (Beck 1967). Only 1997 during the period of 1985–2013 had such a dry period during the spring, but we have no flight observations for that year. The 12-day delay in flight of 1990 relative to the simulated emergence could be caused by its dry March conditions.

Neither observations ($r^2 = 0.00$) nor simulations ($r^2 = 0.14$) could explain the variation in the slope of flight regressed on pupation. This finding supported
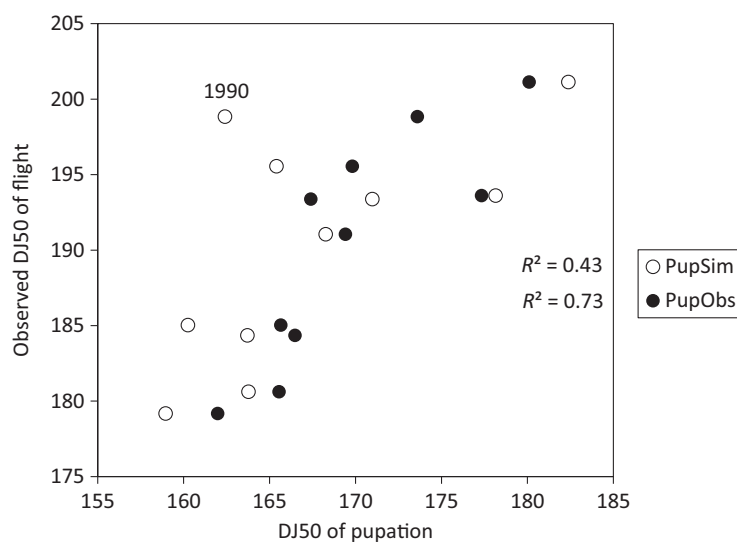

Fig. 5 Mean observed days from January 1 (DJ50) to flight vs. mean simulated and observed days from January 1 to pupation for all years at Changins (VAL3).

our choice to evaluate the model through its simulations of mean pupation (JD50) rather than of the start of pupation.

Conclusions

The use of over 29 years of 1ECB observations permitted the evaluation of currently practiced flight predictions based on observations compared with predictions based on our simulations. For this comparison, two criteria were applied: biases of predictions and their random errors. The results provide confidence to applied biometrics of post-diapause development. We consider these results to be the first to be published on European 1ECB (Maiorano 2011).

The predictions of 1ECB flight based on currently practiced phenological observations were more prone to biases than were predictions based on our simulations. The validation revealed methodological changes in observations, demonstrating risks of including bias in the predictions based on currently practiced phenological observations. The 15.4% (61.2 DD) simulation bias of pupation during the VAL1 validation is an example of this risk. Indeed, local microclimatic conditions during post-diapause development of the pest are difficult to standardize. Consequently, the chosen semi-field conditions of crates containing stalks may not be representative of the field. The model simulates post-diapause phenology without being prone to methodological changes.

As a drawback, predictions of 1ECB flight based on our simulations are more prone to random errors than are predictions based on currently practiced phenological observations. One cause is that the model begins its simulations on January 1, whereas the observations are performed in June. The closer observations are to the beginning of flight, the more precise they are; furthermore, the longer simulations are, the less accurate they become. A predetermined biofix could improve their accuracy, but the model approach would move towards the observation-based approach, with its labour. Another cause of random errors in simulations is the presumption that only temperature influences 1ECB development. The model would be improved if it considered that extended dry periods prolong diapause.

The biases and random errors of our simulations are similar between calibration sites and other sites. Our model performs well in all maize-producing areas of Switzerland. Simulations consider the Swiss landscape with local weather station sites or using a landscape model (Schaub et al. 1995). MeteoSwiss has more than 130 weather stations, while AgroMeteo (Viret et al. 2011) contains 150 stations. The latter stations are more densely distributed in agricultural areas, and the first stations offer more reliable data. Current parasitoid releases are based on phenological observations of only one site. The simulated JD50 value of pupation in low/warm, calibration, typical and high/cool maize-growing areas (Geneva 412, Changins 455, Payerne, St. Gallen 775 m.a.s.l.) was average during 1985–2013 at days 154, 158, 162 and 176, respectively. A consideration of the landscape by the model predictions should at least compensate for its random errors. Predictions based on observations at Changins are 18 days too early every year at St. Gallen. Predictions based on simulations at Changins during one of the 18 years were less than 11 days early, and this error should be similar at other sites. Multiple observation sites would also reflect local conditions and introduce methodological errors and labour to which observations are subjected. The labour of observations at one site (2 weeks work) is already much higher than those of simulations (<1 day). Instead of observations, simulations can profit from weather predictions. Rearing companies and producers should welcome the decreased risk of untimely releases, and Agroscope would appreciate the reduction in its workload.

In practice, the timing of mean pupation and beginning of emergence, that is, flight, does not leave sufficient time (54 DD or approximately 7 days) for parasitoid delivery. Because of this practical constraint, delivery is currently initiated by the beginning of pupation, 168 DD, or approximately 21 days, before the beginning of emergence. The model was validated with JD50 simulations, but any cumulative density proportion can be chosen to predict the beginning of flight and suit parasitoid delivery. This flexibility allows rearing companies to choose the latest moment to ship parasitoids.

The timing of parasitoid release against bivoltine ECB is particularly complex because of overlapping and desynchronized generations. A phenology model of 1ECB and bivoltine ECB could simulate the timing of all three flights. Development of the bivoltine race of Switzerland was studied (Derron et al. 2009), and the literature containing the biometrics of ECB in the USA is available (Maiorano 2011). Due to the unknown proportion of the two races in the field, validation of a model would be challenging.

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