A modelling approach to describe the *Anthonomus eugenii* (Coleoptera: Curculionidae) life cycle in plant protection: a priori and a posteriori analysis

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**Abstract**

*Anthonomus eugenii* Cano (Coleoptera: Curculionidae) is one of the most severe pests for sweet and hot varieties of pepper (*Capsicum* spp.; Solanaceae). The species is distributed widely, principally in Central America, but in 2013 it was detected for the first time in the Lazio region of Italy. Modelling plays a key role in reducing chemical treatments used on *Capsicum* spp., but reliable predictions of pest populations require adjusted tools, as well as intense knowledge of the insect’s biology and its typical environment. The main goal of this work is to describe the life cycle of *A. eugenii* with a physiologically based model, which links the population dynamics with the environmental parameters. More specifically, this analysis focuses on the different response of the age-structured model in relation to the development rate function in input. Two methodologies to determine the best representative development rate function suitable for simulations are proposed; the first is “a priori analysis,” whereas the second is the “a posteriori analysis.” Simulations were compared with semi-field data, collected in a controlled experimental greenhouse where *A. eugenii* developed in varying temperature conditions. Results showed that the model used is adequate to describe *A. eugenii* population dynamics and highlighted how the a posteriori analysis can be essential to (i) analyze the simulation outputs, and (ii) determine the best representing development rate function, if the a priori analysis does not provide this information sufficiently clearly.

Key Words: pepper weevil; Von Foerster’s equation; integrated pest management; alien species; development rate function; physiologically based models

**Resumen**

*Anthonomus eugenii* Cano (Coleoptera: Curculionidae) es una de las plagas más severas para las variedades de chile dulce y chile picante (*Capsicum* spp.; Solanaceae). La especie es distribuida ampliamente, principalmente en América Central, pero en el 2013 se detectó por primera vez en la región italiana de Lazio. El modelado juega un papel clave en la reducción de los tratamientos químicos utilizados en *Capsicum* spp., pero las predicciones confiables de las poblaciones de plagas requieren herramientas ajustadas, así como un conocimiento intenso de la biología del insecto y su ambiente típico. El objetivo principal de este trabajo es describir el ciclo de vida de *A. eugenii* con un modelo basado fisiológicamente, que vincula la dinámica de la población con los parámetros ambientales. Más específicamente, este análisis se enfoque sobre la respuesta diferente del modelo estructurado por edad en relación con la función de tasa de desarrollo en insumo. Se proponen dos metodologías para determinar la mejor función de tasa de desarrollo representativa para usar en simulaciones; el primero es “análisis a priori,” mientras que el segundo es el “análisis a posteriori.” Se compararon las simulaciones con datos de semicampo, recolectados en un invernadero experimental controlado donde *A. eugenii* se desarrolló en diferentes condiciones de temperatura. Los resultados mostraron que el modelo utilizado es adecuado para describir la dinámica de la población de *A. eugenii* y resaltaron cómo el análisis a posteriori puede ser fundamental para (i) analizar los resultados de la simulación y (ii) determinar la mejor función que representa la tasa de desarrollo, si el análisis a priori no proporciona esta información con suficiente claridad.

Palabras Claves: gorgojo de chile; picudo de chile; la ecuación de Von Foerster; manejo integrado de plagas; especies foráneas; función de tasa de desarrollo; modelos basados fisiológicamente

The pepper weevil *Anthonomus eugenii* Cano (Coleoptera: Curculionidae) represents an increasing problem for sweet and hot varieties of pepper (*Capsicum* spp.), not only in Central America (EPPO 2019), its land of origin, but also in Europe where this insect has been discovered recently (Speranza et al. 2014). The first Italian outbreak of the pepper weevil in 2013 (Speranza et al. 2014) was recorded in Fondi and Monte San Biagio, 2 municipalities in the province of Latina (Lazio region). The short development time of *A. eugenii* in favorable conditions and its destructive feeding caused considerable economic losses among pepper producers, arousing the interest of Integrated Pest Management (IPM) scientists. Because *A. eugenii* may develop on both wild and cultivated *Solanum* and *Capsicum* (both Solanaceae) species, insect control strategies often are difficult to implement successfully, because nightshade-
residing populations are able to re-infest cultivated pepper fields the following season (Addesso et al. 2007). Damages are inflicted primarily by the trophic activities of the larvae and adults. In addition, the oviposition behavior of adults cause abortion and fall of flowers (Patrock & Schuster 1992) and infested fruits, causing extensive losses. A complete generation usually requires 20 to 30 d (Capinera 2011), though this is strictly dependent on the optimum climatic conditions. In a laboratory, A. eugenii may reach 8 complete life cycles; however, 3 to 5 generations develop in most pepper weevil native areas (Wu et al. 2019). Indeed, it is common to find adults in the fields from Mar until Jun in the native areas of the pepper weevil, but a certain amount of adults also can be recovered throughout the yr, except for the mo of Dec and Jan (Capinera 2011).

Toapanta et al. (2005) conducted a detailed study describing the response of the pepper weevil to external environmental temperatures, which provided life tables (Harcourt 1969). An external temperature of 30 °C seems to be optimal for egg to adult development time, reproduction, fecundity, and fertility (Toapanta et al. 2005).

A mathematical description of the life cycle of pepper weevil may be of significant importance in planning control strategies to protect pepper crops. In fact, forecasts in agriculture have the potential to provide a general picture of what will happen in the following period. This feature is typical of the Decision Support System (DSS); once simulation results show a trend of an insect pest’s development, experts can fix a threshold beyond which a series of consequences have to be activated in order to implement the appropriate control strategy.

The principal goal of this paper is to describe mathematically the life cycle of pepper weevil, applying the innovative approach described in the work of Rossini et al. (2019a). In particular, this study highlighted the reliability of the model applied in semi-field contexts such as greenhouses, where pepper is usually cultivated in Italy. In addition, an application protocol is proposed in order to improve future applications of physiologically based models. For this purpose, simulation results are compared with unpublished data from an experimental greenhouse located in Fondi (Latina, Italy), in the epicentre of the area that is typically infested.

**Materials and Methods**

**POPULATION MODELLING**

The mathematical details and the computational tools applied in this study are described in the works of Rossini et al. (2019a, b; 2020a). In particular, the model proposed by these authors describes an insect life cycle considering its development over time and through the life stages, and associated with the environmental temperature. The mathematical representation of the model is as follows:

\[
\begin{align*}
\frac{\partial}{\partial t} n(x,t) + \frac{\partial}{\partial x} \left[ \frac{G(x,t)n(x,t)}{\beta(x,t) n(x,t)} \right] &= -M(x,t) n(x,t) \\
n(0,t) &= \int_0^{T_D} \beta(x,t) n(x,t) dx \\
n(x,0) &= n^0(x)
\end{align*}
\]  

where \(x\) and \(t\) indicate physiological age and time, respectively. The expressions \( G(x,t) \), \( \beta(x,t) \), and \( M(x,t) \) represent, in order, the development, fertility, and mortality rate functions usually estimated through laboratory experiments. The physiological age, as described in the work of Rossini et al. (2019a, 2020a), may be associated with the preimaginal stages of the life cycle of A. eugenii.

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The second development rate function to be considered is the Logarithm (Logan & Hilbert 1983):

\[ R[T(t)] = \psi \left[ \exp (\rho T(t)) - \exp \left( \frac{T_M - T(t)}{\Delta T} \right) \right] \]

where \( \psi \) and \( \rho \) are empirical parameters, \( T_M \) is the upper temperature threshold beyond which development is no longer possible, and \( \Delta T \) is the interval width between the maximum peak of the function and \( T_M \).

Hence, there is a synergy between 2 apparently independent models: equation (1) manages the population dynamics, whereas equations (3) and (4) describe the insect’s response to the daily average temperature. Even if equations (3) and (4) are used equally in literature, their mathematical features may provoke different responses in the simulations. In particular, the development rate functions’ parameters are estimated with the same data, but the non-linear fit results may underline a preference for one expression instead of the other. In other cases, it can be difficult to highlight which is the most effective development rate function to use to represent the data. Hence, only a comparison between simulations and field data may determine these differences. This aspect will be discussed in the following section.

**DATA ANALYSIS**

Once the non-linear fit results have provided the functions’ parameters, the choice of the best representative development rate function between equations (3) and (4) will be determined with a \( \chi^2 \)-test and by analyzing the adjusted \( R^2 \)-value. This procedure, together with computational aspects, was described by Rossini et al. (2019a). To estimate the parameters of the expressions (3) and (4) the ROOT’s “Minuit” tool (Brun & Rademakers 2007) was included in an ad hoc C++ program, as reported by Rossini et al. (2020a). As mentioned previously, it may happen that the and values resulting from the non-linear regression with equations (3) and (4) are similar. When this condition is verified, an additional operation is required to assess which is the best representative development rate function for the specific application. In a pre-
liminary analysis, if the non-linear fits results have minor or otherwise
negligible differences, the user could make a direct choice of which
development rate function to use. This statement is supported by the
empirical formulation of both Briére and Logan formulas.

On the other hand, an alternative is to run simulations considering
both the Briére and Logan expressions as development rate functions
as input into equation (1). Simulation outputs then will be compared
with field data, and the most effective development rate function to
use in further applications will be determined a posteriori. The com-
parison between simulation outputs and field data will be conducted
using the methodology described in Rossini et al. (2019a; 2020a, b).
The authors reported that the distance between the simulated and
the actual experimental populations would be evaluated, again con-
sidering the function. As an indicator of the distance, a lower \( \chi^2 \)-value
means a more accurate overlap between simulations and field data.
Accordingly, if the best development rate function to use as input in
equation (1) cannot be selected using the criteria above, it can be help-
ful to compare simulation outputs with field data. Thereafter, the de-
velopment rate function that provides a lower \( \chi^2 \)-value will be applied
in further simulations.

**EXPERIMENTAL DESIGN FOR VALIDATION**

The model validation was conducted during the 2014 growing sea-
son in an experimental greenhouse located in Fondi (Latina, Italy) at
the company GENISTA S.r.l., which specializes in genetic improvement.
The greenhouse had a length of 40 m, a width of 10 m, a minimum
height of 1.95 m, and a maximum height of 3.5 m at the center of
the roof. Pepper plants were transplanted into the greenhouse in Aug,
which was opened to promote *A. eugenii* infestations.

Once the presence of pepper weevils was ascertained inside the experimental
field by visual observations, the greenhouse was isolated with an anti-aphid net (Agritech s.r.l., Eboli, Salerno, Italy) to avoid
the further entrance or exit of *A. eugenii* individuals. At this point,
the adults enclosed in the greenhouse mated and laid eggs on pepper
plants, producing the generation that was monitored to validate and
analyze equation (1).

The monitoring activity focused on pepper weevil adults. For this
purpose, 5 yellow chromotropic sticky traps (Serbios s.r.l., Badia Pole-
sine, Rovigo, Italy) were deployed along the diagonal axis of the field,
and checked each wk from Oct to Dec. The experiment was concluded
at the end of Dec when the pepper fruit was harvested.

The environmental temperature in the greenhouse was recorded
from the date the pepper plants were transplanted until the inter-
ruption of the experiment. More specifically, a meteorological station
placed in the greenhouse provided the daily average temperature
based on 24 measurements (1 every h).

The error associated with the experimental population (dots in
Figs. 1 & 2) is related to sampling time. Normally, this value is fixed at
half the temporal range between the 2 field surveys, which is ± 3.5 d.

**Results**

The life tables provided by Toapanta et al. (2005) facilitated the es-
timation of the development rate function parameters. The best-fit pa-
rameters for equations (3) and (4) are listed in Table 1, together with \( \chi^2 \)
and \( R^2 \) values. Figures 3 and 4 provide a graphical representation of the
best-fit functions. Additional information (correlation matrix, variances and covariances matrix, and a plot of the adjustment curves with 95% confidence intervals) are reported in the supplementary materials.

The criteria for selecting the best development rate function to use
for simulations, as described in the “Data Analysis” section, requires a

![Fig. 1. Simulation output from the model (1) evaluating the daily average temperature with the Briére development rate function.](image)

![Fig. 2. Simulation output from the model (1) evaluating the daily average temperature with the Logan development rate function.](image)
by the development rate function equations, it is possible to determine that these results are, in fact, in accordance with each other.

Simulation results are reported in Figures 1 and 3. In particular, Figure 1 reports the simulation output compared with field data considering the Briére equation as input. In this case, the projections indicate a maximum peak of the population on 22 Nov, whereas field data confirmed that the maximum occurred on 23 Nov. The same situation was reported for the Logan equation, as shown in Figure 4.

The principal differences between the 2 simulations are concentrated in the right-hand side of the plot, on the decreasing tails of the graph. Table 2 reports the $\chi^2$ and $R^2$ values and: whereas the first value indicates the distance between simulations and field data, the second value is helpful for understanding the extent to which the simulations represent the actual greenhouse population. On the basis of the values in Table 2, it is possible to assess that simulations are more reliable if, in equation (1), the response of *A. eugenii* to the daily average temperature is evaluated by the Logan equation.

**Discussion**

The results obtained highlight that the Logan equation (inserted into equation [1]) is more appropriate to describe *A. eugenii* populations. This is not true for all insect species, and it depends on several aspects. For example, the non-linear fit results with equations (3) and (4) are strongly dependent on the number of experimental points in the life tables. Accordingly, enriching the life tables with additional points can increase the accuracy of the first part of the analysis. Besides demonstrating and analyzing these results, this work aims to provide an operating protocol to apply physiologically based models, which requires a combination of a population dynamics model and a phenological model. Specifically for this work, population dynamics is managed by equation (1), while the phenology (in this case, the relationship between insects and environmental temperature) is managed by the development rate function expressions.

An additional result, as demonstrated above, is the utility of the a posteriori analysis. It has, in fact, been shown that when it is impossible to decide prior to the simulation the most appropriate development rate function to use as input in the population dynamics model, the a posteriori analysis is the only viable means of reaching a decision in this respect.

As already anticipated, both Briére and Logan equations are formulated on an empirical basis; there are no reasons to prefer one instead of the other because they represent the life tables in a similar way. On the other hand, the a posteriori analysis showed that even if they represent the life tables in a similar way, the simulation outputs can report more discernible differences.

The considerations resulting from this study are helpful for model scientists who aim to provide tools for direct applications in integrated pest management. The use of mathematical models as a decision support system is growing, and its application has been found in several case studies (Rupnik et al. 2019), most of which are sponsored by government programs (Carberry et al. 2002). For instance, there are models which consider not only the potential abundance of pests...
Table 2. Numerical evaluation of the differences between the simulation outputs and the field data. In this case, $\chi^2$ indicates the distance between simulations and field data, whereas $R^2$ indicates how much the simulation represents field data.

| Development rate function in input into the model | $\chi^2$-value | $R^2$-value |
|--------------------------------------------------|--------------|------------|
| Brière                                           | 1.8231       | 0.9604     |
| Logan                                            | 1.1135       | 0.9797     |

in the field, but also include population density in relation to certain economic thresholds (Tang & Cheke 2008). Despite the existence of various proposals for the mathematical representation of population dynamics (Nance et al. 2018; Ainsel et al. 2011; Rossini et al. 2019b, 2020b), the reliability of the simulations is strongly dependent on the function which relates the species with its environmental parameters. Accordingly, it is not the best method to choose a priori a specific development rate function. Instead, the development rate functions should be evaluated twice: (i) a priori to exclude wide differences in representing life table data, and (ii) a posteriori to evaluate potential differences between different functions in input.

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References Cited

Addesso KM, McAuslane HJ, Stansly PA, Schuster DJ. 2007. Host-marking by female pepper weevils, Anthonomus eugenii. Entomologia Experimentalis et Applicata 125: 269–276.

Aineba B, Picart D, Thiéry D. 2011. An innovative multistage, physiologically structured, population model to understand the European grapevine moth dynamics. Journal of Mathematical Analysis and Applications 382: 34–46.

EPPO – European Plant Protection Organisation. 2019. EPPO Global Database. https://gd.eppo.int/taxon/ (last accessed 6 Jan 2020).

Brière J-F, Pracros P, Le Roux A-Y, Pierre J-S. 1999. A novel rate model of temperature-dependent development for arthropods. Environmental Entomology 28: 22–29.

Brun R, Rademakers F. 2007. ROOT User’s guide: 6 release cycle. https://root.cern.ch/guides/users-guide (last accessed 19 Jan 2020).

Cairnera J. 2011. Pepper weevil, Anthonomus eugenii Cano (Insecta: Coleoptera: Curculionidae). UF/IFAS Extension Publication EENY-278. University of Florida, Gainesville, Florida, USA.

Carberry PS, Hochman Z, McCown RL, Dalgliesh NP, Foale MA, Poulton PL, Har-greaves JNG, Hargreaves DMG, Cawthry S, Hillcoat N, Robertson MJ. 2002. THE FARMSCAPE approach to decision support: farmers’, advisers’, researchers’, monitoring, simulation, communication and performance evaluation. Agricultural Systems 74: 141–177.

Harcourt DG. 1969. The development and use of life tables in study of natural insect populations. Annual Review of Entomology 14: 175–196.

Ikemoto T, Kiritani K. 2019. Novel method of specifying low and high threshold temperatures using thermodynamic SSI model of insect development. Environmental Entomology 48: 479–488.

Logan JA, Hilbert DW. 1983. Modeling the effects of temperature on arthropod populations, pp. 113–122 In Lauenroth WK, Skogerboe GV, Flug M (eds.), Developments in Environmental Modelling. Vol. 5 – Analysis of Ecological Systems: State-of-the-Art in Ecological Modelling. Elsevier Science Publishers, Amsterdam, Netherlands.

Mirhosseini MA, Fathiopour Y, Reddy GVP. 2017. Arthropod development’s response to temperature: a review and new software for modeling. Annals of the Entomological Society of America 110: 507–520.

Nance J, Fryxell RT, Lenhart S. 2018. Modeling a single season of Aedes albopictus populations based on host-seeking data in response to temperature and precipitation in eastern Tennessee. Journal of Vector Ecology 43: 138–147.

Patrock RJ, Schuster DJ. 1992. Feeding, oviposition and development of the pepper weevil, (Anthonomus eugenii Cano), on selected species of Solanaceae. Tropical Pest Management 38: 65–69.

Rossini L, Severini M, Contarini M, Speranza S. 2019a. A novel modelling approach to describe an insect life cycle vis-à-vis plant protection: description and application in the case study of Tuta absoluta. Ecological Modelling: 108778. doi.org/10.1016/j.ecolmodel.2019.108778.

Rossini L, Severini M, Contarini M, Speranza S. 2019b. Use of RooT to build a software optimized for parameter estimation and simulations with Distributed Delay Model. Ecological Informatics 50: 184–190.

Rossini L, Severini M, Contarini M, Speranza S. 2020a. EntoSim, a RooT-based simulator to forecast insects’ life cycle: description and application in the case of Lobesia botrana. Crop Protection 129: 105024. doi.org/10.1016/j.cropres.2019.105024.

Rossini L, Contarini M, Speranza S. 2020b. A novel version of the Von Foerster equation to describe poikilothermic organisms including physiological age and reproduction rate. Ricerche di Matematica. https://doi.org/10.1007/s11587-020-00489-6.

Rupnik R, Kukar M, Vračar P, Košir D, Pevec D, Bosnić Z. 2019. AgroDSS: a decision support system for agriculture and farming. Computers and Electronics in Agriculture 161: 260–271.

Speranza S, Colonelli E, Garonna AP, Laudonia S. 2014. First record of Anthonomus eugenii (Coleoptera: Curculionidae) in Italy. Florida Entomologist 97: 844–845.

Tang S, Cheke RA. 2008. Models for integrated pest control and their biological implications. Mathematical Biosciences 215: 115–125.

Toapanta MA, Schuster DJ, Stansly PA. 2005. Development and life history of Anthonomus eugenii (Coleoptera: Curculionidae) at constant temperatures. Environmental Entomology 34: 999–1008.

Wu P, Haseeb M, Diedrick W, Ouyang H, Zhang R, Kanga LHB, Legaspi JC. 2019. Influence of plant direction, layer, and spacing on the infestation levels of Anthonomus eugenii (Coleoptera: Curculionidae) in open jalapeño pepper fields in North Florida. Florida Entomologist 102: 501–508.