A temperature-dependent phenology model for *Apanteles subandinus* Blanchard, parasitoid of *Phthorimaea operculella* Zeller and *Symmetrischema tangolias* (Gyen)

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Abstract
The potato tuber moth (*Phthorimaea operculella* Zeller) is a major invasive pest of potato (*Solanum tuberosum* L.) worldwide. Classical biological control using parasitoids had been of primary interest during the last decades to control this pest. More than twenty parasitoid species have been reported parasitizing *P. operculella*. *Apanteles subandinus* Blanchard had been successfully used in different countries. Determination of the parasitoid's temperature-dependent development is crucial for better predicting the potential of the parasitoid to establish in a new region and to control the target pest. Therefore, the effect of temperature on the development and reproduction of *A. subandinus* was studied at five constant temperatures ranging from 11–30°C in its main host *P. operculella*. The Insect Life Cycle Modeling (ILCYM) software was used to fit nonlinear equations to collected life table data and to establish an overall phenology model to simulate life table parameters based on temperature. The parasitoid completed its life cycle at constant temperatures from 15 to 30°C. Temperature of 11°C was lethal to pupae, and at 35°C no larvae development was possible. The theoretical lower threshold temperatures for the development of egg-larvae and pupae were 10.3°C and 11.8°C respectively. The model predicted limits for survival at around 12°C and 33°C. The lowest senescence rate was observed within the temperature range of 15–25°C. Oviposition time decreased significantly with increasing temperature from 12.2 days (15°C) to 1.8 days (30°C). The highest fertility was predicted at 27°C. Maximum population growth is expected around 26.78°C with a finite rate of increase, \( \lambda \) of 1.0445, which corresponds to a population doubling time of 15.9 days. The highest values for gross reproduction rate (GRR) and net reproduction rate (R0) were found between 24 and 25°C, and the shortest mean generation time (T) was observed at 30°C (23.48 d). The use of the phenology model in the context of classical biological control of *P. operculella* is discussed.

Keywords
classical biological control, life table statistics, mapping of suitable release areas, modelling, natural enemies, potato pests
1 | INTRODUCTION

The potato tuber moth (Phthorimaea operculella Zeller) (Lepidoptera, Gelechiidae) probably originated from tropical mountainous regions of South America. It has become a cosmopolitan invasive potato pest in more than 90 countries worldwide and is reported the most damaging insect pest of potato (Solanum tuberosum L.) in almost all tropical and subtropical regions of the world. The Andean potato tuber moth, Symmetrischema tangolias Gyen), originated in the mountainous regions of Peru and Bolivia. It is widely distributed at midelevation in the Andes in Colombia, Ecuador, Peru and Bolivia, but its presence has been also reported in Australia, Tasmania, New Zealand and Indonesia (Kroschel & Schaub, 2013). S. tangolias has been shown to be much less invasive than P. operculella, which is adapted to a wider range of agroecological zones and higher temperatures (Sporleder, Schaub, et al., 2016). Chemical control has been the most frequent control method used by farmers worldwide compromising farmer’s health (Orozco et al., 2009) and the environment (Devine et al., 2008), although good examples of integrated pest management for potato tuber moths had been developed (Kroschel et al., 2020) and implemented in different countries (e.g. Australia: Horne et al., 2008; Horne & Page, 2008; Peru: Keller, 2003; Republic of Yemen: Kroschel, 1995).

Classical biological control using parasitoids had been of primary interest during the last decades to control P. operculella. More than 20 parasitoid species of the families Braconidae (11 species), Encyrtidae (2 species) and Ichneumonidae (9 species) have been reported parasitizing P. operculella (Kroschel & Schaub, 2013; Lloyd, 1973). Apanteles subandinus Blanchard, Orgilus lepidus Muesebeck (Hymenoptera: Braconidae) and Copidosoma koehleri Blanchard (Hymenoptera: Encyrtidae) – which have very likely co-evolved with P. operculella in South America – had been widely and successfully used in different countries, e.g. South Africa (Watmough et al., 1973; Whiteside, 1981), Australia (Salehi, 1998; Horne, 1990), Zambia (Crueckshank & Ahmed, 1973), Zimbabwe (Mitchell, 1978), India (Khande et al., 1979, recd. 1982; Pokharkar & Jogi, 2000), Japan (Toguchi, 1999) and Italy (Pucci et al., 2003). A. subandinus, C. koehleri and Macrocentrus ancyliivora Rohwer (Hymenoptera: Braconidae) are the only species reported to parasitize S. tangolias in Peru (Tenorio, 1996; Vera, 1999), but no classical biocontrol programme has been reported for this potato pest.

Temperature is one of the most important factors affecting the development, survival and reproduction rates of insect pests and hence strongly determines demographic parameters, which are required for understanding population growth and dynamics, development rates and seasonal occurrence (Bale et al., 2002; Logan et al., 1976; Uvarov, 1931). Detailed temperature effects on the population growth potentials of P. operculella and S. tangolias are well-known through extensive field and laboratory studies (Keller, 2003; Kroschel & Koch, 1994; Roux & Baumgartner, 1995). Moreover, temperature-based phenology models have been developed and validated for both pests (Sporleder et al., 2004, Sporleder, Schaub et al., 2016) and used to map the pest’s establishment risk and growth potentials in potato regions worldwide under current and future climates influenced by climate change (P. operculella: Kroschel et al., 2013; Kroschel, Sporleder, et al., 2016; S. tangolias: Sporleder, Carhuapoma, et al., 2016).

For properly planning classical biocontrol programmes based on the use of parasitoids and understanding their potential to establish in new environments as well as to successfully control the target pests, it is important to understand the temperature-dependent development of both the host (pest) and the parasitoid and their possible synchrony of development under different climatic (temperature) conditions. Cardona and Oatman (1975) conducted constant temperature experiments but did not develop an overall temperature-dependent phenology model for A. subandinus. The objective of the present study was to determine the nonlinear relationship between temperature and A. subandinus development, survival and fecundity through constant temperature experiments and to use the established phenology model for mapping and assessing the potential use of the parasitoid in classical biocontrol programmes globally. For this purpose, A. subandinus life table data were collected at six constant temperatures in its main host P. operculella. For model validation, additional life table data were collected for three generations of the parasitoid at fluctuating natural temperature conditions.

2 | MATERIALS AND METHODS

2.1 | Origin and rearing of A. subandinus

The specimens used in this study were derived from the laboratory colony maintained at the International Potato Center (CIP), Lima, Peru. Although the parasitoid had been originally reported to occur in Peru (Tenorio, 1996; Vera, 1999), it could not be identified in extended surveys carried out in the main potato growing regions during 2006. Hence, a colony was introduced from Australia in the year 2007 through a Phytosanitary Import Permit (Servicio Nacional de Sanidad Agraria del Perú: file No. 01035 - 2007 · AGSENASA- DSVSCV).

A rearing method for larval parasitoids of P. operculella was established. Reared adults were maintained at 25 ± 1°C, >70% relative humidity and natural photoperiod. Thirty pairs of A. subandinus were placed in a parasitizing chamber (transparent ethylene boxes of a size of 40 × 20 × 20 cm) and fed with a solution of honey and water (in a ratio of 1:2). After 2 days of mating, three slices of potato (variety Yungay) infested with >30 neonate larvae of P. operculella were placed inside the chamber. After 2 days of parasitism, the potato slices were removed and transferred to 0.5-litre plastic containers (between two or three slices per container) and incubated at room temperature until the emergence of A. subandinus adults. After approximately 20 days, developed adults were recuperated by sucking the individuals with an aspirator.
2.2 | Origin and rearing of *P. operculella*

Eggs of *P. operculella* were obtained from a colony maintained at the International Potato Center (CIP) on potato tubers (variety Peruanita) at room temperature (23–26°C), 60%–70% relative humidity and natural photoperiod. After hatching, neonate larvae were placed in plastic containers (30 × 20 × 7.5 cm) containing potato tuber as food and sand as a pupation medium. Pupae were recovered approximately after 20 days, disinfected in 0.3% sodium hypochlorite solution and placed in oviposition cups (½ litre) covered with cheesecloth. A filter paper on the cheesecloth provided an oviposition site for new adults. Adults were fed with 5% sugar solution dropped on top of the cheesecloth. The filter paper was changed daily, and eggs employed for further rearing or bioassays.

2.3 | Experimental procedure and data collection

The effect of temperature on the development and reproduction of *A. subandinus* was studied in controlled incubation chambers (Thermo Fisher Scientific Inc., MA) at five constant temperatures of 11, 15, 20, 25 and 30°C. Data loggers (Hobo H8, Onset, MA) were used to monitor the temperature conditions. Relative humidity in the chambers was maintained at about 60% by placing containers with water; the photoperiod was kept at 12:12 (L:D) h.

2.3.1 | Development of immature stages and survival

For *A. subandinus*, observations on successful parasitism and egg development are not possible without the dissection of *P. operculella* larvae. Therefore, depending on the temperature under study, every 12 hr at 30°C, because development from egg to larva was realized in <12 hr, and every 24 hr at all lower temperatures, 30 larvae were dissected to evaluate and determine parasitism rate and the development of eggs to larvae until all eggs had hatched. Development of parasitoid larvae could be observed within host larvae by using the stereo microscope. The study was carried out as follows. Two hundred 3-day-old larvae of *P. operculella*, individually put on small potato squares (1.0 × 1.0 × 0.4 cm), were placed in 8 L containers with 40 pairs of *A. subandinus* after a period of 1 day of mating. After 12 hr of parasitism at the temperature used for general rearing (25°C), the potato squares were placed in small plastic containers with a volume of 2 cm³ and stored in incubators at the five constant temperatures. For each temperature, not less than one hundred *P. operculella* larvae were inspected using the stereo microscope. Larvae were observed until pupation to determine the larval development time as well as to record survival. When larvae of *A. subandinus* entered the pupae stage, remaining parts of the potato square were removed, and pupae maintained at the same constant temperature conditions until the emergence of adults. Adult emergence was recorded twice daily to determine development time of pupae and sex. This made it possible to evaluate total immature development time for both males and females of *A. subandinus*. When the *A. subandinus* larva was not visible under the stereo microscope, the moth larva was dissected to verify whether it was parasitized. In the life table, egg development time was included in the larva development time (egg-larva). The experiment was repeated three times.

2.3.2 | Adult longevity

At the day of emergence, adults were sexed, isolated and placed in small glass tubes (10 × 50 mm), with a mesh on top and fastened with a rubber band. Adults were fed with a solution of honey and water in a ratio of 1:2. The glass tubes containing the adults were placed in incubators at the five constant temperatures, and observations on survival time were made daily until all insects had died. The mean survival time was recorded for both sexes, and the inverse of it was plotted against the respective constant temperature.

2.3.3 | Reproduction capacity

At the day of emergence, one female and two males were jointly released in a plastic container of 0.5 L and incubated at the five constant temperatures. Adults were fed with a solution of honey and water in a ratio of 1:2. The provided copulation time depended on the temperature (Table 1). After this period, three potato slices infested with 50 larvae were put in the container and replaced in different time intervals depending on the temperature until the female had died (Table 1). To record the parasitism rate, the larvae were reared under the same temperature conditions up to the emergence of adults of *P. operculella* and *A. subandinus*; the number of female and male parasitoids was recorded. The experiment was also used to record the longevity of mated adults. The experiment had 10 repetitions and was at least three times replicated at the different constant temperatures in time. However, at 11°C, no experiments were carried out due to the mortality of pupae of 100% (Table 2).

| Temperature (°C) | Copulation time | Food replacement (days) |
|-----------------|-----------------|-------------------------|
| 11              | 5 days          | 11                      |
| 15              | 3 days          | 6                       |
| 20              | 1.5 days        | 3                       |
| 25              | 1 day           | 1                       |
| 30              | 6 hr            | 0.5                     |
TABLE 2 Mean development time (±SE), mortality and model fitted to development time of immature A. subandinus life stages reared on P. operculella at constant temperatures

| Temperature (°C) | Egg-larvae | Pupae | Total |
|------------------|------------|-------|-------|
|                  | n          | Median dev. time (days) | Mortality (%) | n | Median dev. time (days) | Mortality (%) | Median dev. time (days) | Mortality (%) |
| 11               | 162        | 86.119 (±7.982)a         | 93.2        | - | -                      | -              | -                      | -              |
| 15               | 204        | 34.236 (±3.335)b         | 45.1        | 112| 20.335 (±0.336)a       | 37.5          | 54.58 (±4.513)         | 65.7          |
| 20               | 254        | 16.753 (±1.632)c         | 50.0        | 127| 9.824 (±0.219)b        | 21.3          | 26.57 (±2.318)         | 60.7          |
| 25               | 248        | 10.219 (±0.988)d         | 33.5        | 165| 5.927 (±0.126)c        | 15.8          | 16.15 (±1.218)         | 44.0          |
| 30               | 155        | 7.055 (±0.73)e           | 55.5        | 69 | 4.056 (±0.139)d        | 58.0          | 11.11 (±1.103)         | 81.3          |
| Model            | Log-logistic | Log-logistic           |            |    |                        |               |                        |               |
| Commune slope    | 13.9276     | 16.6667                  |            |    |                        |               |                        |               |
| p(>|z|)          | <0.001      | <0.001                   |            |    |                        |               |                        |               |
| AIC              | 2076.646    | 967.2107                 |            |    |                        |               |                        |               |

Numbers in parenthesis are standard errors.

Mean followed by different letters in the same columns are significantly different (p < .05; Tukey test). Egg-larvae: F = 1669.1; df = 4,479; p < .0001. Pupae: F = 2375.3; df = 3,335; p < .0001.

2.4 | Data for model validation

The influence of fluctuating temperature on the development of immature stages, mortality, survival time of adults and reproduction of A. subandinus was studied under natural temperature conditions from October to December 2010 at the experimental station of CIP in La Molina, Lima (12° 05′ S, 76° 57 W, 250 m a.s.l.) following the same procedure as used in the constant temperature studies. During this period, a total of three generations were observed. A data logger was used to monitor the daily maximum and minimum temperature conditions.

2.5 | Model parameterization and analysis

The development of the A. subandinus phenology model and its life table parameter simulation was conducted using the Insect Life Cycle Modeling (ILCYM) software version 4.0 developed by CIP (Sporleder et al., 2020). The ILCYM software uses R statistics (R Core Team, 2018) for all statistical calculations and is freely available from the institute’s website (www.cipotato.org/ilcym) (Sporleder et al., 2017). Data collected in the life table studies under constant temperature conditions were arranged in incomplete life table formats as required by the ‘model builder’ of ILCYM to process, analyze and develop the phenology model (development time and its variation, development rate, senescence, mortality, total oviposition and relative oviposition frequency). The ‘validation and simulation’ module of ILCYM was applied for simulating life table parameters and for model validation. The best-fit model was selected based on the Akaike Information Criterion (AIC), a well-known goodness-of-fit indicator (Akaike, 1973). The smaller the value of the AIC, the better the model fitted. For the selection of the best functions, statistical criteria and biological aspects of the species were considered (Sporleder et al., 2013).

2.5.1 | Development time and its distribution

For development times and adult longevity, log-error distributions were assumed; the log-logistic, lognormal and Weibull model were tested as distribution link function, and the most appropriate distribution link function was chosen according to the maximum likelihood. ILCYM provides several different models that are adequate for describing the relationship between temperature and median development time, mortality, adult senescence, oviposition time and average fecundity per female. These functions generally are fitted in terms of rates (1/median time); however, in ILCYM and in this study, the functions were fitted in terms of ln-times. In addition, lower developmental thresholds and the thermal requirements for each life stage were calculated by means of linear regression between temperature and observed development rates (Campbell et al., 1974). The AIC provides more information on the distribution of the data and the appropriateness of the model. The life table data were transformed into interval censored time to event data (the events occurred between two observation times) in ILCYM. The data on development time of the different immature life stages, adult longevity and fecundity of females were submitted to survival analysis. Because the data are interval censored, medians cannot be assessed correctly. Parametric accelerated failure time (AFT) modelling (Kalbfleisch & Prentice, 2002) allows to determine medians most correctly and in addition allows to determine the distribution of development times. AFT models were adjusted to the data using the survreg procedure of the survival package in R statistics (Therneau, 2020; Therneau & Grambsch, 2000).

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package were adjusted by regression to describe the mortality rate in each life stage and fecundity by temperature. Development rate was expressed by the reciprocal of the mean development times for immature stages of *A. subandinus*. Mortality was calculated from the frequency of cohort mortality.

2.5.2 Simulation of life table parameters at constant temperatures

Life table parameters – i.e. net reproduction rate (*R₀*), gross reproduction rate (GRR), intrinsic rate of increase (*r_m*), finite rate of increase (*k*), mean generation time (*T*) and doubling time (*DT*) – were estimated using the simulation tool in ILCYM (Southwood & Henderson, 2000; Sporleder et al., 2013). The estimates were based on the phenology model formed to simulate development, mortality and reproduction of 100 individuals for a 1-year period. Deterministic simulation was performed over a range of 11–30°C in 1°C steps.

2.5.3 Model validation

The validation tool in ILCYM was used to evaluate the ability of the developed phenology model to reproduce the *A. subandinus* life table data collected under fluctuating temperature conditions. Differences in development times, mortality rates and life table parameters namely the net reproduction rate (*R₀*), gross reproduction rate (GRR), mean generation time (*T*), intrinsic rate of natural increase (*r_m*), finite rate of increase (*k*), and doubling time (*DT*) between simulated and observed life tables were statistically evaluated by using *z*-scores and *t*-statistics: 

\[ z = (\text{observed value} - \text{simulated value}) / \text{standard deviation of the simulated value}. \]

2.6 Mapping suitable release regions

For mapping suitable release regions, we implemented the presented *A. subandinus* phenology model in ILCYM’s potential population distribution and risk mapping module following the methodology described by Sporleder et al. (2017, 2020) and Kroschel et al. (2013, 2016). For analyzing the potential establishment and efficacy of *A. subandinus* to control *P. operculella* in potato regions globally, we used the Establishment Index (EI) and Generation Index (GI), and generated a new index based on the differences in generations (ΔGI = GIparasitoid - GIfhost) developed annually by the parasitoid and its host *P. operculella* in the different potato growing regions. The three indices are simulated and displayed for potato production regions for which the potential establishment and distribution of *P. operculella* has been confirmed (i.e. with an Establishment Risk Index [ERI] of >0.7, according to Kroschel et al., 2013, 2016). For the spatial simulations, we used temperature data for the year 2018 (CRU-TS 4.03) provided by Harris et al. (2014) and downscaled with WorldClim 2.1 (Fick & Hijmans, 2017) (https://www.worldclim.org/data/monthlywth.html).

3 RESULTS

3.1 Development and its distribution

At the incubation period of 35°C, the development of *A. subandinus* eggs was observed, but thereafter a 100% mortality of larvae occurred and development could not be further evaluated. Likewise, the incubation temperature of 11°C was lethal to pupae and did not allow for a development to adults. Complete development of *A. subandinus* could be evaluated at all other incubation temperatures from 15 to 30°C (Table 2). The duration of the immature stages and the time required to complete the cycle from egg to adult decreased significantly with increasing temperatures. Egg-larva development was twelve times longer at 11°C (86.1 d) than at 30°C (7 d), and pupae development was five times longer at 15°C (20 d) than at 30°C (4 d) respectively. The variation in development times among individuals in the immature life stages across all temperatures was best described by using a log-logistic distribution link function for egg-larvae and pupae, with high significant common scale parameters (for each life stage *p* < .001), based on the lowest AIC values, to describe variability in the development from egg-larvae and pupae according to temperature. The common slopes determined for each life stage were highly significant (*p* < .001) and seem adequate to describe the overall variability in the development within each immature life stage (Table 2, Figure 1).

3.2 Development rate

Temperature-dependent median developmental rates were well described by the Taylor model (Taylor, 1981) for the egg-larvae stage and the modified Janisch-1 model (Janisch, 1932) for the pupae stage (Table 3). The linear model was not suitable to correctly describe the rate of development at extreme temperatures. Therefore, by using AIC selection criteria a nonlinear Taylor model and Janisch-1 model were fitted between the rate of development and temperature. The models explained >97% of the variation in median development times by temperature in each stage (Table 3, Figure 2). The fastest development estimated by the parameter *T*_opt in the Taylor model was at 33°C for egg-larvae and 31°C by the parameter *T*_opt in the Janisch-1 model for pupae respectively. The linear regression suitably described the relationship between temperature and development rate of *A. subandinus*, corroborated by the high *R*². Estimated theoretical lower threshold temperature (estimated from the slope and intercepts of the linear regression) for the development of egg-larvae and pupae were 10.3°C and 11.8°C respectively. Based on these thresholds, the thermal constant (k) for the development, expressed in degree-days (*DD* = 1/slope), was 144.927536 and 75.7575758 for egg-larvae and pupae respectively.
Immature mortality

Mortality showed significant differences among treatments for stages of egg-larvae \( F = 1669.1, df = 4, 479, p < .0001 \) and pupae \( F = 2375.3, df = 3, 335, p < .0001 \). Pupae were the most susceptible immature stages to temperature variation. Egg-larvae mortality was high at extreme temperatures (94% and 100% at 11 and 35°C, respectively), with lowest mortality at 25°C. For pupae, mortality rate was highest at 11°C (100%), and lowest at 25°C (16%) and 20°C (21%) respectively. The total immature mortality had the lowest value at 25°C (44%) and the highest at 30°C (81%). The effects of temperature on the mortality of A. subandinus immature stages egg-larvae and pupae were best described by the Wang 1 model (Wang et al., 1982) (Table 4, Figure 3). The model predicted increasing mortality as temperature deviates from the optimum temperature, indicating limits for survival at around 12 and 33°C (Figure 3).
### 3.4 Adult longevity and fecundity

The sex ratio was highly affected by temperature, with a predominance of males at lower temperature of 15°C (1:6.6 for female: male), and a sex ratio of almost 1:1 at a temperature range of 20°-30°C. The longevity of adult female and male *A. subandinus* decreased with increasing temperature (Table 5), with significant differences between 30°C (12 days for both females and males) and all other temperatures. From 15° to 25°C, longevity of females ranged from 38 to 31 days and of males from 35 to 30 days respectively. No significant differences were observed between female and male longevity. The cumulative frequencies of the adult’s life span and temperature were plotted against normalized developmental times by fitting a Weibull model distribution curve for female and male (Table 5). A

![Graph showing temperature-dependent development rates for immature life stages of *A. subandinus*.](https://example.com/graph1)

![Graph showing temperature-dependent mortality rates of immature life stages of *A. subandinus*.](https://example.com/graph2)

### Table 4 Model and their parameters fitted to describe mortality rate for immature life stages of *A. subandinus* reared on *P. operculella*

| Life stage | Model | Parameters | $F$-value | df | $p$ |
|------------|-------|------------|-----------|----|-----|
| Egg-larvae | Wang 1 | $m(T) = \frac{1}{(1+exp(-x-x_{opt}/B))(1+exp(-T_{opt}-x)/B)).H)}$ | $T_{opt}$ 22.333 $(\pm 1.025)^b$ | 21.78 | 2.4 | 0 |
| | | | B 3.923 $(\pm 0.794)$ | 4.939 | 0.008 |
| | | | H 0.10 $(\pm 0.032)$ | 3.162 | 0.025 |
| Pupae | Wang 1 | $m(T) = \frac{1}{(1+exp(-x-x_{opt}/B))(1+exp(-T_{opt}-x)/B)).H)}$ | $T_{opt}$ 21.927 $(\pm 0.357)$ | 61.5 | 2.3 | 0 |
| | | | B 2.443 $(\pm 0.325)$ | 7.514 | 0.002 |
| | | | H 0.0301 $(\pm 0.012)$ | 2.599 | 0.04 |

*a* Wang 1: where $m(T)$ is the rate of mortality at temperature $T$ (°C), $T_{opt}$ is the temperature at which the development rate is at maximum, and $B$ and $H$ are the fitted parameters.

*b* Numbers in parenthesis are standard errors.
Hilber and Logan 3 model was fitted to determine the relationship between senescence rates of female adults and temperature, and for male adults, an exponential model was selected (Table 6, Figure 4). The lowest senescence rates were observed within the temperature range of 15–25°C.

The AFT model revealed a significant effect of temperature on the oviposition time. Median oviposition time decreased significantly with increasing temperature from 12.2 days at 15°C to 1.8 days at 30°C (Table 5). The effects of temperature on fecundity were described by the Wang 10 model with predicted highest fecundity at 27°C (Table 6, Figure 5a). The relationship between temperature and survival time of adult *A. subandinus* females and males and oviposition rate were best described by an exponential model (Table 6, Figure 5b). Fecundity per female was variable, ranging from zero at 11°C to 45 eggs at 30°C. A Tukey test revealed significant differences between fecundity across all temperatures ($F = 9.8302$, $df = 5$, 107, $p < .001$).

**Table 5** Median survival time, median oviposition time and model fitted to describe development time of *A. subandinus* adults reared on *P. operculella* at constant temperatures

| Temperature (°C) | Longevity (days) | Median oviposition time (days) | Mean fecundity (eggs/female) |
|------------------|-----------------|-------------------------------|-----------------------------|
|                  | Female          | Male                          | Female                      | Male                          |
| 15               | 37.969 (±3.423) | 35.496 (±3.718)               | 12.21 (±2.416)               | 15.9 (±2.55)                  |
| 20               | 34.001 (±3.830) | 32.599 (±4.323)               | 6.221 (±1.524)               | 25.8 (±2.62)                  |
| 25               | 31.156 (±3.381) | 30.226 (±3.867)               | 2.204 (±0.584)               | 31.7 (±6.68)                  |
| 30               | 12.30 (±2.091)  | 11.846 (±2.423)               | 1.823 (±0.408)               | 38.6 (±5.23)                  |
| Model            | Weibull         | Weibull                       | Wang 10                     |
| Commune slope    | 3.115264        | 2.717391                      |
| p (>z/)          | <0.001          | <0.001                        |
| AIC              | 1508.498        | 1607.646                      | 50.649                      |

*a* Numbers in parenthesis are standard errors.

*b* Mean followed by different letters in the same columns are significantly different ($p < .05$; Tukey test). Female: $F = 14.905; df = 3, 192; p < .0001$. Male: $F = 10.942; df = 3, 139; p < .0001$. Oviposition: $F = 8884.37; df = 3, 2768; p < .0001$.

**Table 6** Estimated parameters of the nonlinear models fitted to describe the relationship between temperature and adult senescence rates, oviposition rate and fecundity for *A. subandinus* reared on *P. operculella*

| Response variable | Model* | Parameters | $F$-value | $df_{1,2}$ | $p$   |
|-------------------|--------|------------|-----------|------------|-------|
| Female senescence rate | Hilber and Logan 3 | $r(T) = \text{trid}((T - T_{\text{min}})/(T_{\text{max}} - T_{\text{min}})^2 + D)\cdot \exp(-(T_{\text{max}} - (x - T_{\text{min}}))/D_{t}) + S_{\text{min}}$ | 65,010.46 (±0) | 0.528 | 5.11 | 0.749 |
|                   |        | $\text{trid}$ | 38.567 (±0) | 18.153 (±3.008) | 94.591,199 (±0) | 0.017 (±0) | 0.024 (±0.009) | 0.024 (±0.009) |
|                   |        | $T_{\text{max}}$ | 38.567 (±0) | 18.153 (±3.008) | 94.591,199 (±0) | 0.017 (±0) | 0.024 (±0.009) | 0.024 (±0.009) |
|                   |        | $T_{\text{min}}$ | 38.567 (±0) | 18.153 (±3.008) | 94.591,199 (±0) | 0.017 (±0) | 0.024 (±0.009) | 0.024 (±0.009) |
|                   |        | $D$ | 38.567 (±0) | 18.153 (±3.008) | 94.591,199 (±0) | 0.017 (±0) | 0.024 (±0.009) | 0.024 (±0.009) |
|                   |        | $D_{t}$ | 38.567 (±0) | 18.153 (±3.008) | 94.591,199 (±0) | 0.017 (±0) | 0.024 (±0.009) | 0.024 (±0.009) |
|                   |        | $S_{\text{min}}$ | 38.567 (±0) | 18.153 (±3.008) | 94.591,199 (±0) | 0.017 (±0) | 0.024 (±0.009) | 0.024 (±0.009) |
| Male senescence rate | Exponential simple | $r(T) = b_1 \cdot \exp(b_2 \cdot T)$ | 0.009 (±0.006) | 5.174 | 1.3 | 0.151 |
| Oviposition rate | Exponential simple | $l(T) = b_1 \cdot \exp(b_2 \cdot T)$ | 0.0112 (±0.006) | 34.428 | 1.3 | 0.028 |
| Fecundity | Wang 10 | $n(T) = \exp(a \cdot (1 - \exp(-(x - Tl)/Bl)) \cdot (1 - \exp(-(Th - x)/Bh)))$ | 0.791 (±0.452) | 2.001 | 2.6 | 0.481 |
|                   |        | $a$ | 0.791 (±0.452) | 2.001 | 2.6 | 0.481 |
|                   |        | $Tl$ | 36.966 (±1.114) | 2.001 | 2.6 | 0.481 |
|                   |        | $Th$ | (−30.512 (±0.005) | 2.001 | 2.6 | 0.481 |
|                   |        | $Bl$ | 923.114 (±0.131) | 2.001 | 2.6 | 0.481 |
|                   |        | $Bh$ | 9.385 (±3.58) | 2.001 | 2.6 | 0.481 |

*a* Exponential simple: $r(T)$ is the senescence rate at temperature $T$ (°C), where $b_1$ and $b_2$ are equation parameters. $l(T)$ is the oviposition rate at temperature $T$ (°C), where $b_1$ and $b_2$ are equation parameters. $l(T)$ is the oviposition rate at temperature $T$ (°C), where $b_1$ and $b_2$ are equation parameters. $n(T)$ represents the fecundity function at temperature $T$ (°C), and $a$, $Tl$, $Th$, $Bl$, $Bh$ are parameters of the equation.

*b* Numbers in parenthesis are standard errors.
3.5 | Life table parameters

Simulations of *A. subandinus* population parameters show that the intrinsic rate of natural increase \( r_m \) augmented almost linearly with increasing temperature representing an asymmetrical dome-shaped pattern to reach a maximum at 26.8°C (0.04356745) and decreasing sharply at 30°C (0.01587048), with a minimum value at 17.44°C (0.00000429) (Figure 6a). Maximum population growth is expected at around 26.78°C with a finite rate of increase, \( \lambda \) of 1.0445 (Figure 6b), which corresponds to a population doubling time of 15.9 days (Figure 6e). The highest values for both reproductive parameters: gross reproductive rate (GRR) (Figure 6c) and net reproductive rate (\( R_0 \)) (Figure 6f) were found between 24°C and 25°C. The shortest mean generation time (T) was observed at 30°C (23.48 days) (Figure 6d).

3.6 | Validation of the model

Phenology model validation of *A. subandinus* was carried out using fluctuating temperature data at a range from 18–33°C, with an average mean temperature of 24.8°C. Simulated population parameters were mostly well predicted when compared with observed data collected under fluctuating temperature. The most significant discrepancy was with the mean generation time (Table 7).

3.7 | Suitable release regions

An Establishment Index (EI) = 1 indicates survival and reproduction of *A. subandinus* throughout each day of the year, which means that the likelihood of long-term establishment for classical biological control is very high (Figure 7). Regions with a very high potential for successful releases (EI >0.9) in countries invaded by *P. operculella* are in Central America (e.g. Mexico), Africa (e.g. Ethiopia, Kenya, Rwanda, Sudan, Tanzania and Madagascar), Asia (India, Nepal and Indonesia) and northwest Australia. However, *A. subandinus* was successfully established in subtropical regions with an EI >0.5–0.9 (light green to orange zones) as in Argentina, Cyprus and other regions of Australia. This high establishment potential is associated with a Generation Index (GI) >13 (up to 28 generations) in tropical and >9–13 generations in subtropical regions, which are potentially developed by *A. subandinus* per year (Figure 8). Moreover, the number of generations developed by *A. subandinus* per year strongly surpass the generation numbers of its host *P. operculella* by >6–15 generations in tropical and >2–6 generations in subtropical regions, respectively, indicating an overall good biocontrol potential and capacity of *A. subandinus* in these regions (Figure 9).

4 | DISCUSSION

Development, survival and reproduction in insect species are dominated by temperature (Brown et al., 2004). Establishing temperature-dependent functions for these parameters permit assembling full life cycle insect models with temperature as the main input variable. Among the examples for experimentally establishing all required functions describing an insect’s life history are the models established for the main hosts of *Apanteles subandinus*, *Phthorimaea operculella* (Sporleder et al., 2004) and *Symmetrischema tangolias* (Sporleder, Schaub, et al., 2016). This approach has been also used for parasitoids used as biological control agents, for example, for *Lysiphlebia mirzai* Shuja-Uddin, a parasitoid of *Toxoptera citricida* Kirkaldy (Liu & Tsai, 2002), *Anagyrus pseudococci* Girault, attacking the vine mealybug [*Planococcus ficus* (Signoret)] (Daane, 2004) and *Diadegma anurum* (Thomson), attacking *Plutella xylostella* L. (Golizadeh et al., 2008).

Preliminary studies to understand the effects of temperature on the development of *A. subandinus* were conducted by Cardona and Oatman (1975). In the present study, we investigated the temperature dependence of all physiological processes of *A. subandinus* in its main host *P. operculella* over the full range of temperatures in which the species is expected to develop. The established functions describing the temperature-dependent development, survival and oviposition allowed the development of an overall *A. subandinus*
phenology model. Life table parameters simulated at constant temperatures indicated that *A. subandinus* population develops within the temperature range of 13°C to 30°C, with an optimum temperature of 25°C. These findings are supported by the study of Cardona and Oatman (1975) confirming that *A. subandinus* does not tolerate temperatures above 32°C. The intrinsic rate of increase indicates the most favourable temperature for population growth (i.e. development time, survival and reproduction; Southwood & Henderson, 2000). Minimum and maximum temperature thresholds for population development were determined at 17.44°C and 30°C, with a maximum population growth at 26.78°C ($\lambda = 1.0445$). Also, at 25°C, the finite rate of population increase was highest and doubling time shortest. Finite rate of increase and doubling time are the most important parameters describing population increase. Validation of the phenology model was conducted by comparing modelling results with life table data of three generation cycles obtained from studies with fluctuating temperatures at a range from 21 to 30°C. Development time and population parameters were properly predicted by the model. However, significant deviations occurred for the mean generation time slightly overestimating the intrinsic rate of increase. More data at extreme temperatures could be supportive to increase the precision of estimated parameters.

Mortality of *A. subandinus* was significant different among temperatures. Egg mortality was difficult to assess as development occurred inside host larvae. Immature stages of *A. subandinus* were shown to tolerate a different thermal range. Egg development was successful at all evaluated temperatures while larvae development was not possible at 35°C, and pupae developed only in the range of 15–30°C. According to Mahroof et al. (2003), each insect stage has a different metabolic rate, which allows for the production of proteins protecting the stage against thermal stress. The longevity of females and males in our study was lower...
than reported by Cardona and Oatman (1975) and Kfir (1981) for *A. subandinus*. This could be due to the high humidity (>60%) in our study, which negatively affects insect longevity (Emana, 2007; Evans, 1983). According to Roux and Baumgartner (1995) and Lightle et al. (2010) also nutrition can be a possible cause for the reduction of adult longevity and the production of progenies. Sporleder et al. (2004) emphasized that larval nutrition and light intensity may affect oviposition and adult senescence and may mask the effect of temperature.

In classical biological control programmes for *P. operculella*, *A. subandinus* was released as an exotic parasitoid mostly in combination with the encyrtid *Copidosoma koehleri* and the braconid *Orgilus lepidus*. The parasitoids established in several countries, but the control efficacy was not consistent among the regions (Cañedo et al., 2016). Understanding the parasitoids likelihood for establishment in new target environments as well as their population growth potential is crucial for effectively planning and implementing classical biocontrol programmes. Failure of biological control programmes has been deeply influenced by climatic factors (Messenger and van den Bosch, 1971). It has been therefore proposed that biological control agents are best obtained from areas where climatic conditions match the areas in which they are to be released (Hoelmer & Kirk, 2005). As a result, climate-matching techniques have been used in biological control to identify climatically suitable regions for biological control agents to be released on invasive alien plants (Byrne et al., 2002; Sutherst et al., 2007). Another approach is the use of complex phenological models, which form a thorough basis for developing deductive species distribution models (Orlandini et al., 2019). This approach is applied in the model builder of the Insect Life Cycle Modeling (ILCYM) software (www.cipotato.org/ilcym; Sporleder et al., 2013, 2020), which have been used in the present study to develop the phenology model for *A. subandinus*. ILCYM is linked to a Geographic Information System (GIS)-based application that contains basic tools for mapping and managing geographic information. Cañedo et al. (2016) already successfully implemented the presented *A. subandinus* phenology model in ILCYM’s potential population distribution and risk mapping module. Developed maps on global, regional and national scales of countries in Africa demonstrate where *A. subandinus* could be potentially introduced and established under current (year 2000) and future climates (year 2050), also indicating its control efficacy (based on the numbers of generations developed/year), and potential population increase and spread in regions where its main host *P. operculella* is established or may expand its distribution due to climate change (Kroschel, Mujica, et al., 2016; Kroschel, Sporleder, et al., 2016; https://cipotato.org/riskatlasforafrica/ilcym/).

Classical biological control of *P. operculella* and hence releases of *A. subandinus* should be considered in potato production regions in which *P. operculella* has been permanently established, causing significant economic damage in potato fields and stores. Therefore, the three indices (establishment index [EI], generation index [GI] and ∆GI [i.e. difference between generations developed

\[ \text{FIGURE 6} \quad \text{Simulated life table parameters of } A. \text{subandinus using the phenology model at constant temperatures. (a) Intrinsic rate of natural increase } (r_m), \text{ (b) finite rate of increase } (\lambda), \text{ (c) gross reproduction rate (GRR), (d) mean generation time (T), (e) doubling time (Dt) and (f) net reproduction rate (R_o) [Colour figure can be viewed at wileyonlinelibrary.com]} \]

\[ \text{FIGURE 6} \quad \text{Simulated life table parameters of } A. \text{subandinus using the phenology model at constant temperatures. (a) Intrinsic rate of natural increase } (r_m), \text{ (b) finite rate of increase } (\lambda), \text{ (c) gross reproduction rate (GRR), (d) mean generation time (T), (e) doubling time (Dt) and (f) net reproduction rate (R_o) [Colour figure can be viewed at wileyonlinelibrary.com]} \]
by the parasitoid and its host]) applied in this study to identify suitable release areas for the parasitoid A. subandinus were only displayed in potato production regions globally for which the potential establishment and distribution of its primary host P. operculella has been confirmed (Kroschel et al., 2013, 2016). Good biocontrol agents produce large numbers of offspring, and ideally, parasites complete more than one generation during each generation of the pest (Meyer, 2003). Therefore, the difference in numbers of generations (ΔGI) of a parasitoid and its host, which are developed per year could be considered as a valuable indicator for the potential control efficacy of a biocontrol agent where higher ΔGI values would indicate a larger biocontrol capacity. According to the developed maps, potentially suitable release areas for A. subandinus with a high control efficacy are tropical

### TABLE 7

| Average daily temperature range | 1st cycle | 2nd cycle | 3rd cycle |
|--------------------------------|-----------|-----------|-----------|
|                                | 21°C–30.4°C | 21°C–30.4°C | 22.8°C–27.3°C |
| **Life table parameters**     |           |           |           |
| Intrinsic rate of increase (r) | 0.012 (±0.046) | 0.024 (±0.013) | 0.023 (±0.027) |
| Net reproductive rate (R₀)    | 2.556 (±2.389) | 2.063 (±3.39) | 3.352 (±3.76) |
| Gross reproduction rate (GRR) | 7.426 (±7.604) | 7.461 (±7.523) | 12.135 (±7.95) |
| Mean generation time (T)      | 31.818 (±0.499) | 30.52 (±3.806) | 26.976 (±1.05) |
| Finite rate of increase (λ)   | 1.012 (±0.046) | 1.024 (±0.013) | 1.023 (±0.028) |
| Doubling time (Dt)            | 36.823 (±131.87) | 29.312 (±1794) | 29.864 (±71.08) |
| **Development time (days)**   |           |           |           |
| Egg-larvae                    | 9.799 (±0.3) | 10.004 (±0.666) | 9.602 (±0.876) |
| Pupae                         | 7.082 (±0.405) | 6.957 (±0.271) | 6.232 (±0.509) |
| **Mortality (%)**             |           |           |           |
| Egg-larvae                    | 0.5 (±0.086) | 0.464 (±0.08) | 0.412 (±0.087) |
| Pupae                         | 0.242 (±0.228) | 0.2 (±0.162) | 0.311 (±0.178) |

*Numbers in parenthesis are standard errors.*

FIGURE 7 Potential establishment and distribution of A. subandinus according to model predictions, using the Establishment Index (EI) for the year 2018 and displayed in potato production regions globally for which the potential establishment and distribution of its primary host P. operculella is confirmed (i.e. with an Establishment Risk Index >0.7). An EI >0.5 indicates regions with potential permanent establishment of A. subandinus and are suitable regions for release [Colour figure can be viewed at wileyonlinelibrary.com]
potato regions, but the use of *A. subandinus* can also be considered in subtropical regions. Good examples of successful releases of *A. subandinus* have been reported from both tropical and subtropical regions (Cañedo et al., 2016), which support the suitability of our mapping results. Although we currently do not have data to determine what minimum value of ΔGI can be considered for high probability of success, these values could be estimated empirically in the future based on reported successful and unsuccessful introductions made in the past and by comparing ΔGI for different biocontrol agents of *P. operculella* or other pests.

In conclusion, the developed phenology model and simulated life table parameters estimated for *A. subandinus* at constant temperatures reflect the temperature-dependent growth potential of the parasitoid in its main host *P. operculella*. Linked to the GIS-based application in ILCYM, it was successfully used to predict suitable release areas globally based on temperature (not considering other abiotic factors such as precipitation or humidity). Thus, the developed phenology model and mapping approach presented here can be used as a new tool to increase the successes of future biological control programmes against *P. operculella* and can be adapted to other pests and natural enemies.
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CONFLICT OF INTEREST
There is no conflict of interest.

AUTHOR CONTRIBUTIONS
Verónica Cañedo, Waldo Dávila, Pablo Carhuapoma and Jürgen Kroschel conceived research. Verónica Cañedo and Waldo Dávila conducted experiments. Jürgen Kroschel, Jan Kreuze contributed material. Pablo Carhuapoma analyzed data and conducted statistical analyses. Verónica Cañedo, Pablo Carhuapoma and Jürgen Kroschel wrote the manuscript. Jürgen Kroschel and Jan Kreuze secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT
Data are openly available in a public repository that issues data sets with DOIs. The data that support the findings of this study are openly available in: Cañedo et al., 2017: https://doi.org/10.1016/S1049-9644(02)00021-X

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