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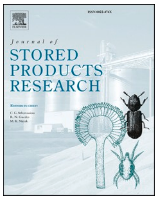

Development of *Bruchus rufimanus* Boheman 1833 (Coleoptera: Chrysomelidae) at different temperatures with special emphasis on rearing and modelling approach

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ABSTRACT

Modelling the thermal response of insect pests is a valuable tool for predicting the stage development of the population, supporting the formulation of more sustainable and effective control strategies. This study focuses on *Bruchus rufimanus*, a specific pest of *Vicia faba* L. responsible for damages caused by larvae that develop inside the seeds. In particular, it tackled the thermal development modelling of this pest in a two-fold approach, given the current lack of information on the cryptic post embryonic development in terms of degree-days. Baseline data were collected by laboratory rearing that considered the insect reproductive diapause and proposed first insights for developing a protocol to rear this pest under controlled conditions. Subsequently, various models were evaluated to describe the effect of different constant temperatures on the embryonic and total development. The effect of temperature on the sex ratio of the next generation was also investigated. The most accurate model for the description of both embryonic and total development was the *Briere-2* model. The temperature thresholds obtained for eggs and total pest developments were 8.2 ± 0.5 °C and 12 °C respectively. Cumulative degree-day requirements were 83°-days for eggs and ranged from 550 to 740°-days for total development. Temperature had no effect on sex ratio. These findings provided a better understanding of the annual development of this pest and might support the future formulation of IPM strategies to control *B. rufimanus*.

1. Introduction

Bruchid beetles (Coleoptera: Chrysomelidae) are pests of dry or immature leguminous seeds (Fabaceae), responsible for important damages worldwide (Southgate 1979; Kingsolver 2004). In the last few years, the Broad Bean Weevil (BBW) *Bruchus rufimanus* Boheman 1833 (Coleoptera: Chrysomelidae) gained particular attention in Europe, given the significant and increasing economic concerns on seeds of faba bean crops, *i.e.* the plant species named *Vicia faba* L. (Fabaceae) (Simmen 2020; Segers 2023).

This small Coleopteran pest has a univoltine life cycle which is closely related to climatic conditions and to the phenology of the host plant (Hamidi et al. 2021). Adults overwinter in wooded sites in reproductive diapause and colonize flowering fields in spring, when temperatures overreach 15 °C (Hoffman et al. 1962). Above this temperature threshold, the adults start to feed pollen and nectar to complete the sexual maturation; after the coupling, females lay their eggs on young forming pods (Segers et al. 2021). According to the current literature, the oviposition starts when temperatures reach 20 °C (Tran and Huignard 1992). Emerging larvae penetrate the pod tissues and settle inside a seed to undergo the larval (four instars) and the pupal development, concurrently to seed formation and maturation (Boughdad 1994). Adults emerge at the end of the season, either before or after the harvest, spending a period of reproductive diapause in forested areas waiting for favourable conditions for the reproduction (Medjdoub--Bensaad et al. 2007; Huignard et al. 2011; Segers et al. 2021).

The larval and pupal development of BBWs inside forming pods leads to a series of harmful consequences for seed quality, such as a decline in nutritional values or flavour quality, a reduced aesthetic value due to necrotic areas and emergence holes on the seed coats, an overall reduced germination capability of the seeds, and an increased risk of fungal contamination during storage or sowing (Boughdad and Lauge 1995; Kaniuczak 2004; Huignard et al. 2011; Khelfane-Goucem and Medjdoub-Bensaad 2016).

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The conventional management of crop infestations by BBWs involves repeated treatments with pyrethroid-based insecticides (Ward and Smart 2011). However, the limited amount of active ingredients available, the restricted number of authorized applications, and the persistence of the phytosanitary products do not ensure a sufficient plant protection. This condition is even more amplified by the more frequent warm climatic conditions and by the egg-laying period of BBW that can extend up to 5 weeks (Ward 2018; Segers et al. 2021). Moreover, conventional spraying methods that provides for a top-down application endorse the accumulation of active ingredients on flowers, with negative consequences on pollinators and other auxiliary insect communities. Conversely, this condition does not affect BBWs, because fertile females lay eggs at the basal nodes of the plant bearing pods, where the concentration of active ingredients is lower (Hausmann et al. 2019; Segers 2023). Consequently, the pressure exerted by weevils has significantly increased over the last decade in Europe, which has led to the collapse of the exportation to Egypt, one of the most fruitful markets for growers (Lacampagne 2021).

Alternative strategies should be urgently planned to control the infestations by this pest in a more sustainable and effective way. Several control strategies have been already considered, such as resistant varieties (Szafirowska 2012; Seidenglanz and Hunady 2016; Carrillo--Perdomo et al. 2019; Dell'Aglio and Tayeh 2023), semiochemical control (Bruce et al. 2011; Leppik et al. 2016; Segers et al. 2023), biopesticides based on essential oils, entomopathogenic fungi (Sabbour et al. 2007; Titouhi et al. 2017; Segers 2023), or even shifts in sowing and harvesting dates that would break the yearly monogenerational cycle of the pest. Mihiretu and Wale (2013) suggested that harvesting seeds before the emergence of BBWs adults, followed by seed treatment, would lead to a reduction of the pest population in the following years. However, quantitative information to anticipate the emergence of BBWs at the end of the seed maturation is still missing. To anticipate the insect's emergence, there is a need for empirical descriptions (*e.g.,* a degree-day-based model) of how temperature affects the post-embryonic development of BBWs inside seeds.

The first field study highlighting the influence of temperature on *B. rufimanus* was carried out by Ward (2018) and showed that temperature may affect overwintering emergence and oviposition, although the data could not provide statistical tangible conclusions. The thermal development of *B. rufimanus* was also investigated by Gailis et al. (2022). However, the degree-days were computed from a hypothetical base temperature of 0 °C that was not supported by *ad hoc* experiments; moreover, the experimentation was carried out under field conditions, where an artificial control of the environmental factors is quite limited. The establishment of a thermal model for the development of BBWs would require the rearing of BBWs populations under different constant temperatures (Quinn 2017), but no baseline information on the establishment of BBW rearing is currently available. Similar studies were instead carried out on some other bruchid species, such as *Bruchus pisorum* L., *Callosobruchus chinensis* L., *C. maculatus*, and *Acanthoscelides obtectus* (Say, 1831) or *A. macrophtalamus* (Park et al. 1991; Smith 1992; Wu et al. 2013; Mobarakian et al. 2014; Soares et al. 2015).

The aim of this study was to provide a series of quantitative information on the thermal response of *B. rufimanus* development under controlled laboratory conditions. This goal was achieved in two steps: the first step focused on the definition of methodological guidelines to establish *B. rufimanus* rearing, while the second step aimed at repeating the rearing under different constant temperatures by focusing on the embryonic and total development (*i.e.*, egg-to-adult). The different development times observed were subsequently converted in development rates, more suitable for a mathematical description and for the comparison of three non-linear models. Finally, the potential influence of temperature on the sex ratio of emerging adults was investigated.

2. Material and methods

2.1. Cultivation of host plants

Spring commercial cultivars of faba bean, named "Tiffany" (RAGT, Rodez, France), were sown in 45 × 50 × 20 cm trays (16 seeds/tray) containing composted soil on a bed of clay balls. Four cylindrical wire meshes were placed in each tray to support plants (Fig. S1 in Supplementary data). Plants were grown in a climatic chamber under conditions of 16 h/8 h photoperiod using 23 W bi-phosphorous white vegeleds ® (Seraing, Belgium) ensuring a minimal light intensity of 150 μmol/m^{2}s for floral induction. This photoperiod was selected to ensure the end of BBW's reproductive diapause, according to Tran and Huignard (1992). The environmental conditions (*i.e.*, temperature and relative humidity) were automatically regulated by a thermostat to ensure full control of the environment. The rearing system provided a light spectrum with a Photosynthetic Active Radiation (PAR) of 98.37%, including 16.16% of blue light, 37.30% of green light, and 44.91% of red light.

To increase precision, the temperatures inside the rearing cages were recorded with a data logger (EasyLog EL-USB-2, LASCAR electronics, Wiltshire, United Kingdom), which collected data every 30 min. The final temperature used in the data analysis was therefore the average of all the values recorded. This choice ensured a constant double check of the conditions inside the growth chambers and a more accurate estimation of the uncertainties associated with temperature.

No fertilizer was provided to plants, and they were regularly watered at their base rather than at the canopy level, to minimise the risk of occurrence of fungal diseases. Three types of phytosanitary interventions were carried out to maintaining the plants in good health conditions for the entire duration of the experimentation: (i) fungicide application with Fungaflor® (imazalil 100 g/l) at the stage GS105 of faba bean (Knott, 1990) to avoid *Oidium* sp. infections, (ii) acaricide application at the stage GS201 with Floramite® (bifezanat 240 g/l) to avoid *Tetranichus* sp. proliferation, and (iii) insecticide application at the stage GS201 with Karate Zeon® (λ-cyhalothrin 100 g/l) to avoid thrips and whitefly infestations. It is worth precising that insecticide applications were carried out at least three weeks before the release of *B. rufimanus* adults in the growth chamber, widely respecting the shortage period and ensuring the correct execution of the experimentation.

According to the literature, faba bean requires a thermal time of 830–1000°-days computed from a base temperature of 0 °C (Patrick and Stoddard 2010). Under climatic chamber conditions of (21 ± 1) °C flowering induction (*i.e.*, flower bud apparition) occurred 40 days after sowing and lasted up to 60 days circa. Given that faba bean has a mixed breeding system requiring insect pollination (Stoddard, 1986; Stoddard and Bond, 1987), manual pollination was carried out to favour the pods formation. The first pods were observed around 60 days after sowing on plants measuring 60 cm in height. Pods maturation lasted until the 106th day after sowing, when pods were ripened.

2.2. Insects' collection and rearing procedure

The continuous rearing of insects ensuring the specimens for the constant temperature trials was carried out as follows. Broad bean weevils in reproductive diapause were collected from harvested faba bean seeds in August and September 2020 at the Gembloux Agro-Bio Tech experimental farm. The adult specimens were caught using emergence trap placed over a container, filled with approximately 400 kg of harvested faba bean seeds, and subsequently placed in boxes having dimensions of 10 cm × 10 cm x 7 cm (100 adults/box) containing corrugated cardboard with a filter paper soaked in 10% sucrose solution at a temperature of (10 ± 1) °C and a constant darkness (hereafter denoted by "overwintering conditions"). Sucrose solution was autoclaved to avoid the risk of moulding and renewed twice a month for each box. Under these overwintering conditions, adults can survive up to eight months (Tran and Huignard 1992). Survival rates under the above-mentioned conditions were observed once a month.

Previous studies showed that at least 80% of adults (both male and female) can overcome their reproductive diapause after a period of seven months under overwintering conditions when they are in presence of their host plant and a photoperiod of 18 h light – 6 h darkness (Tran and Huignard, 1992). Batches of 25 bruchids (15 females and 10 males) were therefore placed in cages (50 × 50 × 120cm) containing 16 flowering faba bean plants supplied by a Petri dish containing pollen stains stuck on a honey imbibed filter paper as supplementary food supply (Fig. S1 in Supplementary data). The rearing conditions in these cages were (22 ± 2) °C, (62 ± 8) % RH and a 16:8 (LD ratio) photoperiod with a light intensity of 185μmol/m^{2}s at the mid-cage height (hereafter denoted by "mating and ovipositing conditions"). The plant development and the insect activity were monitored daily. In particular, the mobility, the feeding, the mating and the oviposition behaviour as well as eggs incubation time were monitored. The observations on cryptic development of larvae were limited until adult's emergences, to avoid destructive samplings. Further generations were then repeated following this procedure under different constant temperatures for thermal modelling.

2.3. *Egg incubations and total developments under different temperatures*

2.3.1. *Egg-to-larva development (embryonic development)*

Eleven batches of pods carrying freshly laid eggs were placed in incubators to assess the thermal effect on egg incubation and to further inspect the different egg substages, a biological information still unclear, at that time. Each pod bearing eggs were daily checked to assess the embryonic development. Incubations were carried out at eleven constant temperatures, namely: (12.4 ± 0.4), (14.9 ± 0.9), (17.7 ± 0.7), (20.5 ± 0.6), (22 ± 1), (23 ± 2), (23.4 ± 0.6), (28.0 ± 0.6), (31.1 ± 0.4), (35.0 ± 0.4), and (40.0 ± 0.4) °C.

2.3.2. *Egg-to-adult development (total development)*

Eight different constant temperatures were tested to explore the egg-adult stage development, namely: (14 ± 2), (17 ± 1), (21.1 ± 0.6), (22 ± 2), (24 ± 1), (27 ± 2), and (28.1 ± 0.8) °C. In this phase, the day zero indicated the day the egg was laid, while the last day corresponded to the emergence of the adult of the new generation from the faba seed. For each constant temperature tested, the delays from first oviposition to adult emergence were recorded, as well as the sex ratio of the next emergence, and the percentage of adults that emerged from seeds. For each rearing cage, the emerging adults were sexed by observation of sexual dimorphism, *i.e.*, the presence of spurs at the extremity of mesotibias and the intended pygydium of male (Segers et al. 2021).

It is known from the literature that generally faba bean do not produce pods above 28 °C (Ellis et al. 1988). Accordingly, the total development at 28 °C was carried out by releasing gravid females in the cage for 5 day at 21 °C, so that they were allowed to lay eggs on forming pods. The adults were then removed from plants and the temperature was increased up to 28 °C for the rest of next generation's life cycle.

2.4. *Thermal development and data analysis*

2.4.1. *Egg-to-larva and egg-to-adult development: life tables values calculation*

The life table values reported as a result of this study were calculated according to Rossini et al. (2024). For each experimental dataset, synthetic values were calculated from the development times of each reared individual, including the mean, the corresponding standard error of the mean, the median (the middle value separating the upper and lower halves of the dataset), the mode (the most frequent value), the kurtosis (thickness of the tails of the distribution), and the skewness (measure of the asymmetry of the distribution).

The thermal accumulation in terms of degree days was computed for each constant temperature, denoted as T_i, (see equation (A1) in Appendix 1). Analogously to the development times, the mean value and the standard error of the mean were calculated, as well as the median, mode, kurtosis, and skewness in terms of degree days.

The dataset corresponding to each constant temperature was graphically represented by plotting the raw data (Rossini et al. 2024), given the greater amount of information deriving from this kind of plot (*e.g.*, minimum amount of day for egg hatching or adult emergence). The calculations were carried out using Matlab (version 2023a).

Sex ratios (F/M) at the different constant temperatures were analysed as follows: first it has been checked the normality of the dataset through the Shapiro-Wilk test, then the data were analysed through Kruksall-Wallis. This part of the analysis was carried out using the RStudio (version 2022.07.1 + 554) and R (version 4.1.2) software.

2.4.2. *Egg-to-larva and egg-to-adult development, mathematical interpretation of development over temperature*

The development times, $D_i(T)$, of each individual i observed at the different constant temperatures were first converted in development rates, $G_i(T)$ (see equation (A2) in Appendix 1).

The development rates over temperature of both egg-to-larva and egg-to-adult provided the typical increasing-decreasing profile that can be mathematically interpolated using the so-called development rate functions. In particular, the literature offers several options (Quinn 2017), but the empirical nature of these functions lets the choice difficult. For this purpose, a preliminary fitting was carried out considering the non-linear models of Logan (Logan et al. 1976), Lactin (Lactin et al. 1995), Briere (Briere et al. 1999), and Sharpe and De Michele (Sharpe et al. 1977) (see equations (A3)-(A6) in Appendix 1). After the preliminary evaluation, the data analysis was oriented towards the functions that provided meaningful results. The non-linear fits were carried out using the fitting library included in the Matlab software (version 2023a), and the goodness of fit was evaluated considering the sum of squares error (SSE), the coefficient of determination (R^2) and the Root Mean Squared Error (RMSE) (Rossini et al. 2020, 2021). All the scripts and the raw dataset to fully reproduce the results of the present study are publicly available at https://github.com/lucaros1190/LifeTables-Bruchusrufimanus (accessed on January 16, 2024).

3. Results

3.1. *Rearing under overwintering, mating, and oviposition conditions*

The observed survivals of diapausing adults under overwintering conditions progressively decreased up to eight months, where the survivals became lower of 50% of the overall overwintering population (Table S1 in Supplementary data).

Once adults were removed from overwintering conditions and placed under mating and ovipositing conditions, it was observed that they stayed immobile for three-four days in the top of cages before they begin to prospect for food, by walking on stem or leaves of their host plants. First feeding behaviours were observed four days after, circa, the placement of adults in rearing cages. Adults fed first on the extrafloral nectaries before they went into flowers (see Fig. A2 a – b in Appendix 2). First couplings were observed (see Fig. A2 c in Appendix 2) eleven days after the placement of adults in rearing cages and was concurrent to the first flying activities. All greening pods were prospected for oviposition after 18 days (see Fig. A2 d in Appendix 2). As the number of gravid females was excessive, if compared to the number of produced pods, a high number of eggs was continuously laid over a period of 40 days. The total number of eggs laid on pods greatly differed between cages and ranged from 627 to 2308, reporting an average fecundity of 97.8 eggs under the assumption that all females had the same survival rate of 100% over the oviposition period.

The egg observations were useful to assess the *Bruchus* species, which may be easily confused by only observing adults' morphology. In the case of *B. rufimanus* eggs, the eggs shape is ovoid, and the translucid chorion is smooth and free of any ornamentation. This allowed the distinction of four morphological stages during the embryonic development of *B. rufimanus* (Fig. 1) (Huignard et al. 2011; Bellifa and Chapelin-Viscardi 2021): *i)* the freshly laid egg with homogenous whitish opaque appearance, *ii)* the mid-grey stage corresponding to the formation of the first tissue of the larvae, *iii)* the black-head stage corresponding to cephalic capsule of the larvae, and *iv)* the hatched egg presenting the exit hole on the pod surface.

First emergences were observed from the 60th day to the 80th day after oviposition (*i.e.*, day where seeds were dissected to check for adults that stayed inside seeds).

3.2. Egg-to-larva and egg-to-adult development: life tables results

This section shows the response of *B. rufimanus* to different constant temperatures. A synthesis of the results of the egg-to-adults development, including observations of oviposition delays as well, sex ratios of the next generation, and percentage of emerging bruchids is reported in Table S2 (Supplementary data).

Eggs showed different distributions of the development times over temperature (see Figure A3.1 in Appendix 3) and, in general, eggs incubation time decreased with increasing temperatures (Table 1). Results assessed that the shortest incubation period for eggs occurred at higher temperatures, reaching a minimum of less than 10 days (cf., 3 days at 35.0 ± 0.4 °C). On the other hand, at low temperatures the hatching time is strongly delayed, requiring until 28 days at (12.4 ± 0.4) °C.

Despite variations in temperatures, all the eggs hatched within a relatively brief timeframe, as highlighted by the standard errors of the mean presented in Table 1. The parameters of the distribution of the development times confirm this result, as both the median and mode values are close to the mean development times.

A different scenario was observed for the egg-to-adult development. The shortest duration for adult emergence was recorded at 28 °C (see Figure A3.2 in Appendix 3), which can also be regarded as the optimal temperature for development based on the synthetic values provided in Table S2 (Supplementary material).

3.3. Influence of temperature on sex ratio

The Kruksal-Wallis test did not reveal any statistical differences among the five different temperatures tested for the sex ratios (F/M) of adults ($\chi^2(4) = 5.47$, $p = 0.241$). A boxplot representation of sex ratio over time is presented in Fig. A4 in Appendix 4.

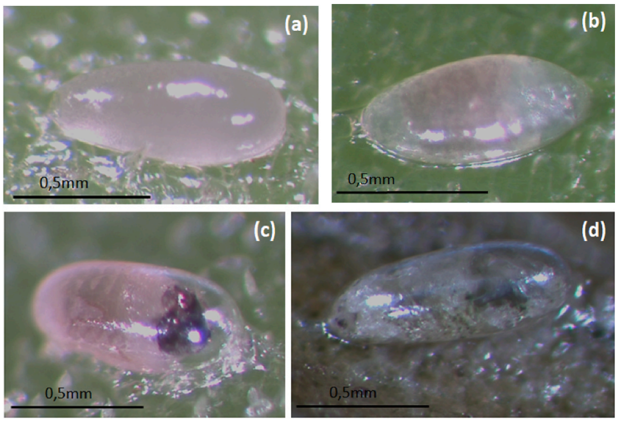

Fig. 1. Different stages of *B. rudimanus* embryonic development (a) Freshly oviposited egg, (b) mid-grey stage, (c) black head stage, (d) hatched egg.

3.4. Egg-to-larva and egg-to-adult development rate functions results

Among the four non-linear models tested, the Lactin function has been discarded from the analysis, given the non-convergence of the fitting algorithm after several attempts. The parameter values for other fitting models (*i.e.*, *Briere 2*, *Logan*, *Sharp and Michele*) are listed in Table 2. The goodness of fit parameters (Table 2) and the biological interpretation of the fitted development curves (Fig. 2) confirmed that the *Briere 2* model is the most reliable one to describe the thermal response of both egg-to-larva and egg-to-adult phases of *B. rufimanus*, with adjusted R^2 of 0.96 and 0.70, respectively.

The lower thermal threshold (T_L) for the egg development was (8.2 ± 0.5) °C, according to the *Briere* equation (the only equation that explicitly contains this parameter). The mean cumulative degree-days required for egg development computed from this T_L value ranged from 83 to 110°-days.

The lower thermal threshold for the egg-adult phase was estimated at 12 °C by the *Briere2* equation. The mean cumulative degree-days required for egg development computed from this T_L value ranged from 550 to 740.

4. Discussion

4.1. Rearing procedure, limits and areas of improvements

This study provided the first protocol to rear *B. rufimanus* under laboratory conditions, emphasizing some insights on the required conditions for the BBW and the host-plant developments. More precisely, the study provided fundamental information on the maintenance of overwintering adults, the lifting of reproductive diapause depending on the host plant flowering, the mating and oviposition on subsequently formed pods, and the *V. faba* flowering and pod-setting under controlled conditions.

The developed rearing procedure was time consuming, and some improvements may be further carried out by setting up two types of artificial diets based on the different feeding behaviour of adults and larvae. An artificial diet that induces the exit of the adults from the reproductive diapause (*e.g.* nectar and pollen from the host plant) could be obtained by placing beehives in field bean crops. It could be expected that immature honey obtained mainly from *V. faba* during the flowering period, along with pollen gathered by pollen traps, could provide the adults the necessary components that were identified by Tran and Huignard (1992) to overcome the diapause. However, the development of an artificial diet for feeding larvae should also consider the different levels of nutrients present in the seeds over the maturation phase, as well as the evolution of proteic/carbohydrates content over the different larval stages. Korsvold (2020) provided quantification of starch, protein, and moisture seed content over the development of the faba bean seed. In particular, they reported a varying moisture seed content (MSC) that range from 82.87% (cf., immature stage) to 32.7% (cf., most matured observed stage), the highest starch concentration (SC) of 40.5% on formed seeds with 55.42 % of MSC, and the lowest SC of 12.1% on forming seeds with 82.87% of MSC. The protein concentration (PC), instead, ranged between 27.5% in formed seeds (*i.e.*, MSC of 55.42%) and 33.4% in immature seeds (*i.e.*, MSC of 82.87%). These indications would provide speculative baseline information for the development of two types of artificial diets: *i)* an artificial diet for egg hatching (*i.e.*, L1 to L3 larval instars), and *ii)* an artificial diet for ~ L3 larval instar up to pupation.

The cryptical pupation prevented a more accurate determination of the end of the egg-to-adult development: it might be possible that, as partially observed in this study, some individuals remain longer inside the seed before emerging. This is probably the reason why different development time distributions were observed over the different tested temperatures and the decreasing R^2 concerning the total development.

Table 1

Results of the eggs-to-larva and eggs-to-adult development under different constant temperatures. Parameters of the distributions obtained from the raw dataset, in terms of development time and degree-day.

			Development times						Degree-days				
Observation (n)	Temp. (°C±SE)	Survival (%)	Mean (days ±SE)	Mode (days)	Med. (days)	Kurt. (days)	Skew. (days)	Cumulative degree-days (°C·days±SE)	Mode (°C·days)	Median (°C·days)	Kurt. (°C·days)	Skew. (°C·days)
Eggs-larva (49)	12.4 ± 0.4	44.90	35 ± 3	34	35	2.26	0.26	85 ± 8	81.6	84.0	2.26	0.26
Eggs-larva (58)	14.9 ± 0.9	87.93	27 ± 1	27	27	3.04	0.03	133 ± 5	132.3	132.3	3.04	0.03
Eggs-larva (61)	17.7 ± 0.7	95.08	13.9 ± 0.6	14	14	10.50	−2.57	107 ± 4	107.8	107.8	10.50	−2.57
Eggs-larva (62)	20.5 ± 0.6	100.00	10.8 ± 0.8	10	11	2.00	0.43	114 ± 9	105.0	115.5	2.00	0.43
Eggs-larva (80)	22 ± 1.0	100.00	9.6 ± 0.6	10	10	2.55	0.16	115 ± 7	120.0	120.0	2.55	0.16
Eggs-larva (102)	23 ± 2.0	98.04	8.4 ± 0.5	8	8	1.05	0.23	110 ± 6	104.0	104.0	1.05	0.23
Eggs-larva (34)	23.4 ± 0.6	100.00	7.8 ± 0.6	8	8	2.64	0.07	105 ± 8	107.2	107.2	2.64	0.07
Eggs-larva (75)	28.0 ± 0.6	100.00	5.9 ± 0.3	6	6	10.58	−3.09	107 ± 5	108.0	108.0	10.58	−3.09
Eggs-larva (71)	31.1 ± 0.4	81.60	4.1 ± 0.3	4	4	6.70	2.38	87 ± 7	84.4	84.4	6.70	2.39
Eggs-larva (111)	35.0 ± 0.4	84.69	3.3 ± 0.5	3	3	3.73	1.32	83 ± 12	75.0	75.0	3.73	1.33
Eggs-larva (70)	40.0 ± 0.4	0.00	–	–	–	–	–	–	–	–	–	–
Eggs-adults (86)	21.1 ± 0.6	–	66 ± 9	56	66	2.08	0.48	600 ± 80	509.6	600.6	2.09	0.48
Eggs-adults (79)	22 ± 2.0	–	68 ± 5	64	67	2.59	0.51	680 ± 50	641.2	671.3	2.59	0.51
Eggs-adults (18)	23 ± 2.0	–	64 ± 6	61	61	1.89	0.40	740 ± 70	702.7	702.3	1.90	0.40
Eggs-adults (49)	27 ± 1.0	–	46 ± 4	49	46	1.83	0.15	670 ± 60	719.8	675.7	1.83	0.15
Eggs-adults (49)	28 ± 1.0	–	35 ± 6	32	32	1.89	0.43	550 ± 90	513.9	513.9	1.90	0.44

Table 2

Best fit parameters of the different equations describing the thermal response of egg and egg to adult of *B. rufimanus*.

Development rate function	Egg incubation		Total development	
	Best fit parameter (±SE)	Goodness of fit parameters	Best fit parameter (±SE)	Goodness of fit parameters
Briere	a=(3.0 ± 0)·10^{-4}	SSE = 0.24	[a]a = 4.3·10^{-5}	SSE = 0.003
	$T_L = 8.2 \pm 0.5$	RMSE = 0.019	[a]$T_L = 12$	RMSE = 0.003
	$T_M = 39.98 \pm 0.01$	$R^2 = 0.96$	[a]$T_M = 33$	$R^2 = 0.70$
	m = 12 ± 2	NDF = 704	[a]m = 5	NDF = 280
Logan	$\psi = 1.18 \pm 0.008 \cdot 10^{-2}$	SSE = 0.23	$\psi = 1 \pm 1 \cdot 10^{-3}$	SSE = 0.003
	$\rho = 9.3 \pm 0.3 \cdot 10^{-2}$	RMSE = 0.018	$\rho = 0.12 \pm 0.04$	RMSE = 0.0003
	$T_M = 42.2 \pm 0.1$	$R^2 = 0.96$	$T_M = 31 \pm 3$	$R^2 = 0.67$
	$\Delta T = 3.0 \pm 0.2$	NDF = 704	$\Delta T = 1 \pm 2$	NDF = 280
Sharpe and De Michele[a]	A = 36	SSE = 0.24	A = 12	SSE = 0.003
	B = 5	RMSE = 0.26	B = −210	RMSE = 0.0034
	C = 40	$R^2 = 0.95$	C = −6	$R^2 = 0.69$
	D = −30	NDF = 702	D = −230	NDF = 278
	E = 57		E = −10	
	F = 681		F = −300	

[a] The uncertainties were not reported because of non-reliable values.

4.2. *Thermal development of B. rufimanus*

The development time ranges that were observed for eggs and total development of *B. rufimanus* in controlled conditions confirmed the indications of different bio-ecological studies (Boughdad 1994; Yus-Ramos et al. 2014; Roubinet 2016; Pölitz and Reike 2019) where incubation times where reported at 1–2 weeks, with most eggs hatching after 10 days. Boughdad (1994) observed a total development time ranging from 90 to 110 days in field conditions, while our results showed that the total development was maximized at 68 ± 5 days under constant temperatures.

Studies on the thermal response have also been carried out for other species of bruchids, such as *B. pisorum*, *C. chinensis*, *C. maculatus*, *A. obtectus* or *A. macrophtalamus* (Park et al. 1991; Smith 1992; Wu et al. 2013; Mobarakian et al. 2014; Soares et al. 2015). On the one hand, literature reports development thresholds and cumulative degree-days for eggs and total development in accordance with the case of *B. rufimanus*. The temperature threshold for *B. pisorum* egg development was estimated at 9.4 °C, which is close to the estimations carried out for *B. rufimanus*. On the other hand, the cumulative degree-days for egg development were relatively lower than other bruchid species: the literature reports 35.15°-days for the case of *C. chinensis* (Maharjan et al., 2017) and 47.2°-days for the case of *B. pisorum* (Park et al., 1991). The total development of *B. rufimanus,* the T_L value and the degree-days (*i.e.*, 12 °C and at least 550°-days) were comparable with the values of other bruchid species, *i.e.*, 10.4 °C and 526.3°-days for *C. chinensis*, 12.8 °C and 632.8°-days for *A. macrophtalamus*, or 11.1 °C and 685°-days for *A. obtectus*.

Recently, Gailis et al. (2022) assessed the thermal development of *B. rufimanus* in field conditions, but their results were affected by

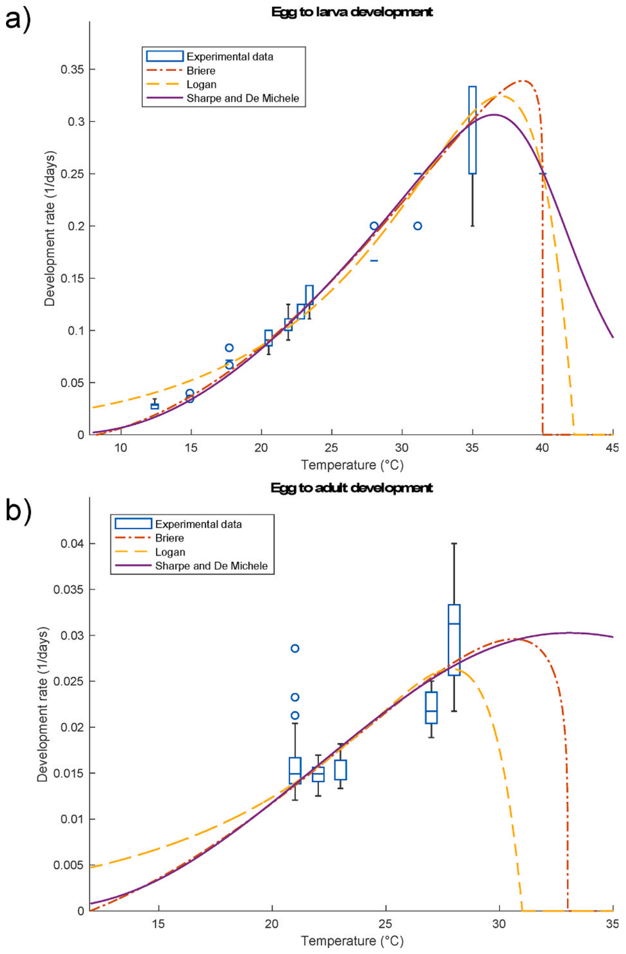

Fig. 2. Best fit functions describing egg incubations (a) and egg to adult developments (b) of *B. rufimanus*.

methodological biases and inaccuracies in the assumptions of the thermal measurements. They considered a base temperature of 0 °C to calculate the thermal development of *B. rufimanus,* which overestimates the actual degree-days required. As showed by this and similar studies carried out on other bruchids species, the base temperature is usually higher. Additionally, temperature was not measured directly on the faba bean crops, but by using the "*closer weather station*". Besides the lack of precision induced by the distance separating field from the weather station, microclimatic crop conditions of BBW post-embryonic development (*i.e.*, pods at the base of the plants) may greatly differ from the temperature measured by a standard weather station placed at height of 2 m (Durigon and de Jong van Lier, 2013; Siebert et al., 2014). This laboratory study has provided more pertinent results on the thermal response of *B. rufimanus,* complementing the study of Gailis et al. (2022).

4.3. Thermal development as potential management tools against B. rufimanus

The problem of the BBW management is related to the endophytic post-embryonic development, as the feeding larvae are difficult to reach with phytosanitary treatments. According to Mihiretu and Wale (2013) and Bachmann et al. (2020), it is possible to reduce the BBW population from year to year by implementing adapted cultural practices, such as early seed harvesting to prevent adult emergence, and by subsequently treating the harvested seeds. The results of this study suggest that a minimum of 550 cumulative degree-days, calculated from the date of the first observation of oviposition in the crop (with a development threshold of 12 °C) should be considered to determine the appropriate harvest time, if seed maturation has been sufficiently reached. Further in-depth studies should validate this assumption by implementing the thresholds in field management programs.

The physiological aspect of faba bean, characterized by indeterminate growth, may limit the seed maturation timing as there is a decline throughout pod formation, which competes with the retention of flowers within the plant (Patrick and Stoddard 2010). When the plant concentrates photoassimilate in the forming seeds rather than in the flowers (*i. e.*, at the end of faba bean flowering), it is common to observe pods showing different levels of maturation. In this scenario, the BBWs may have reached the degree days required for their full development, despite the presence of immature seeds on plants. Early harvesting of seeds with high relative humidity would be highly detrimental to seed storage due to the potential overheating of seeds or the appearance of contaminants such as mycotoxins (Acuña-Gutiérrez et al. 2022), which are not allowed by food or feed standards. In addition, harvesting seeds with a relative humidity above 16% results in escalating drying costs for farmers, depending on the specific level of seed relative humidity (Fegra, 2023).

In this context, the suggested IPM practices that would decrease the interannual BBW populations should be accompanied by a carefully chosen and adapted varietal selection (*e. g.* early varieties). Indeed, the earliness of seed maturity would ensure that a great portion of the seeds are ripe before the onset of BBW emergence. As shown by the seed samples collected in Belgium during the 2021 growing season, all the BBWs were still into the seeds, and emerged only two weeks after the harvesting time (Segers 2023). This fact supports the hypothesis that seeds maturity might be reached before BBWs emergence, namely that there may exist any combinations of climate and cultivar that endorse a faster plant development and seed maturation rather than BBWs. This combination may benefit from the knowledge on BBWs thermal development. Future field experiments aimed at improving the results of this study should also consider the effect of relative humidity of the seed in the model framework. This approach would help to understand if an optimal harvest time can be identified.

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Submission declaration and verification

All authors (A.S., L.R., R.C.M., E.G., F.F) agree to the submission of the present manuscript, which has not been published before and is not concurrently being considered for publication.

CRediT authorship contribution statement

Arnaud Segers: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. **Luca Rossini:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. **Rudy Caparros Megido:** Conceptualization, Methodology, Project administration, Supervision, Validation, Writing – review & editing. **Emanuele Garone:** Formal analysis, Supervision, Validation, Writing – review & editing. **Frederic Francis:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jspr.2024.102352.

Appendix 1. Detailed mathematical description of the development rate functions involved in this study

- Computing the degree day:

$$DD(T_i) = \sum_{n=0}^{N} (T_n - T_L) \tag{A1}$$

where T_L is the baseline temperature calculated through equation (4).

- Conversion of development times, $D_i(T)$, in development rates, $G_i(T)$:

$$G_i(T) = \frac{1}{D_i(T)} \tag{A2}$$

-The Logan development rate function (Logan et al. 1976):

$$G(T) = \psi\left[\exp(\rho T) - \exp\left(\rho T_M - \frac{T_M - T}{\Delta T}\right)\right] \tag{A3}$$

where ψ and ρ are empirical parameters, T_M is the maximum temperature above which the development is theoretically not possible, and ΔT is the temperature range between the maximum of the function $G(T)$ and T_M.

-The Briére development rate function (Briere et al., 1999):

$$G(T) = aT(T - T_L)(T_M - T)^{1/m} \tag{A4}$$

where a and m are empirical parameters, and T_L and T_M are the lower and maximum temperatures below and above which the development is theoretically not possible, respectively.

-The Sharpe and De Michele rate function (Sharpe et al., 1977):

$$G(T) = \frac{T \exp\left(A - \frac{B}{T}\right)}{1 + \exp\left(C - \frac{D}{T}\right) + \exp\left(E - \frac{F}{T}\right)} \tag{A5}$$

where A, B, C, D, E, and F are parameters related to the enzyme kinetics (Rossini et al. 2019).

-The Lactin rate function (Lactin et al. 1995):

$$G(T) = \exp(a\,T) - \exp\left[a\,T_M\left(\frac{T_{M-}T}{\Delta T}\right)\right] \tag{A6}$$

where T_M is the maximum temperature above which the development is theoretically not possible, and ΔT is the temperature range between the maximum of the function $G(T)$ and T_M, a and b are empirical parameters.

Appendix 2. Behavioural observations of *B. rufimanus* reared under controlled conditions

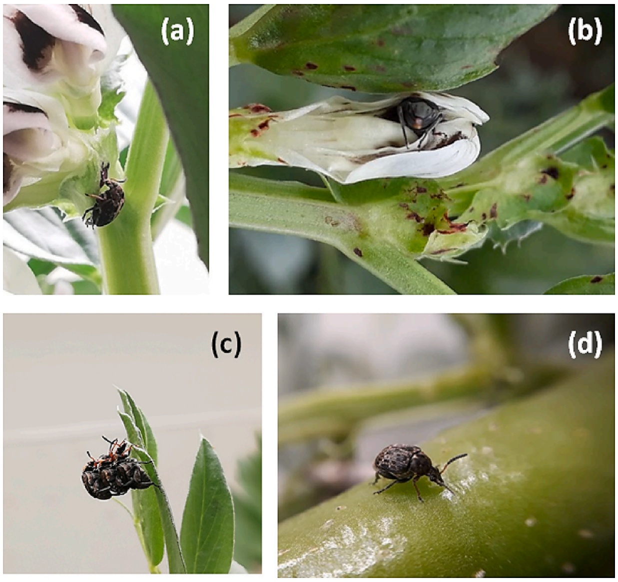

Figure A2. Behavioural observations in *B. rufimanus* rearing, including feeding on flowers or extrafloral nectar (a) and (b), mating (c), and oviposition (d).

Appendix 3. General plots of the egg and total development distributions of the times, and of the sex ratio

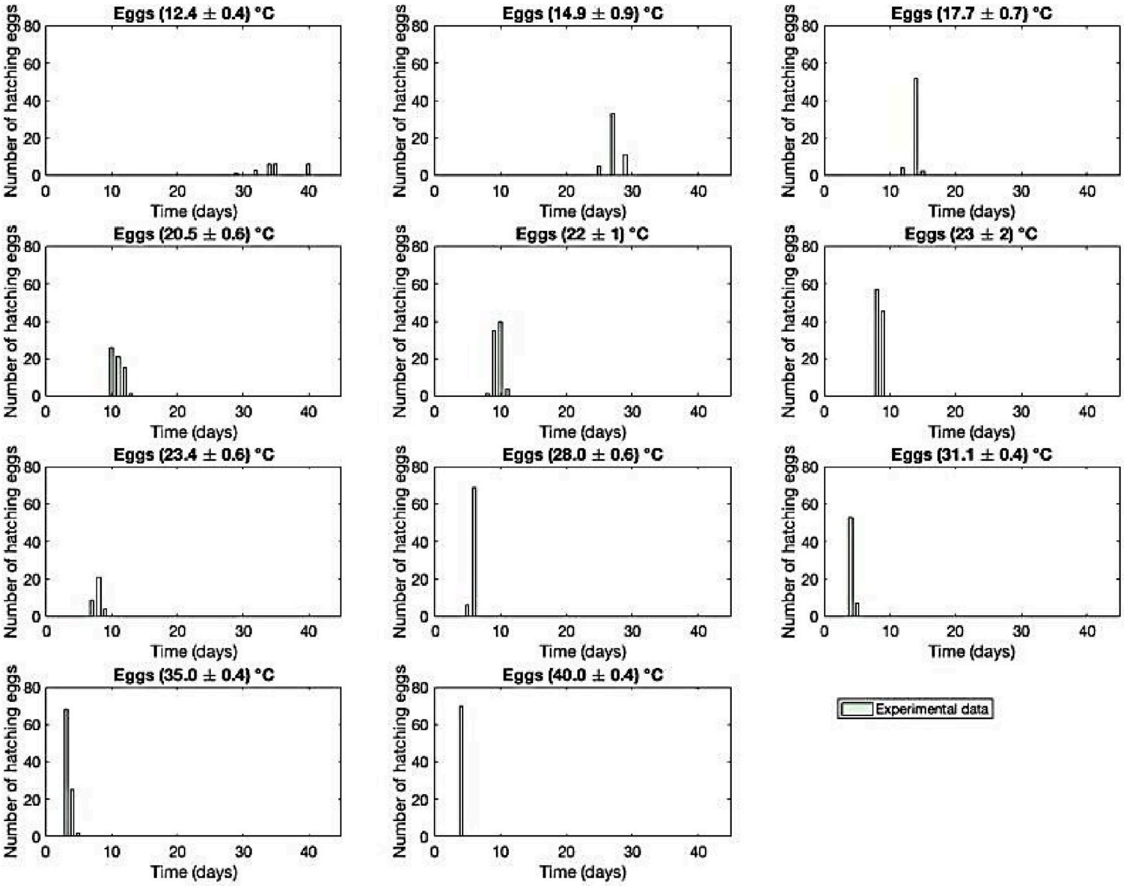

Figure A3.1. General plot of the distribution of the eggs' development times over the different constant temperatures explored in this study.

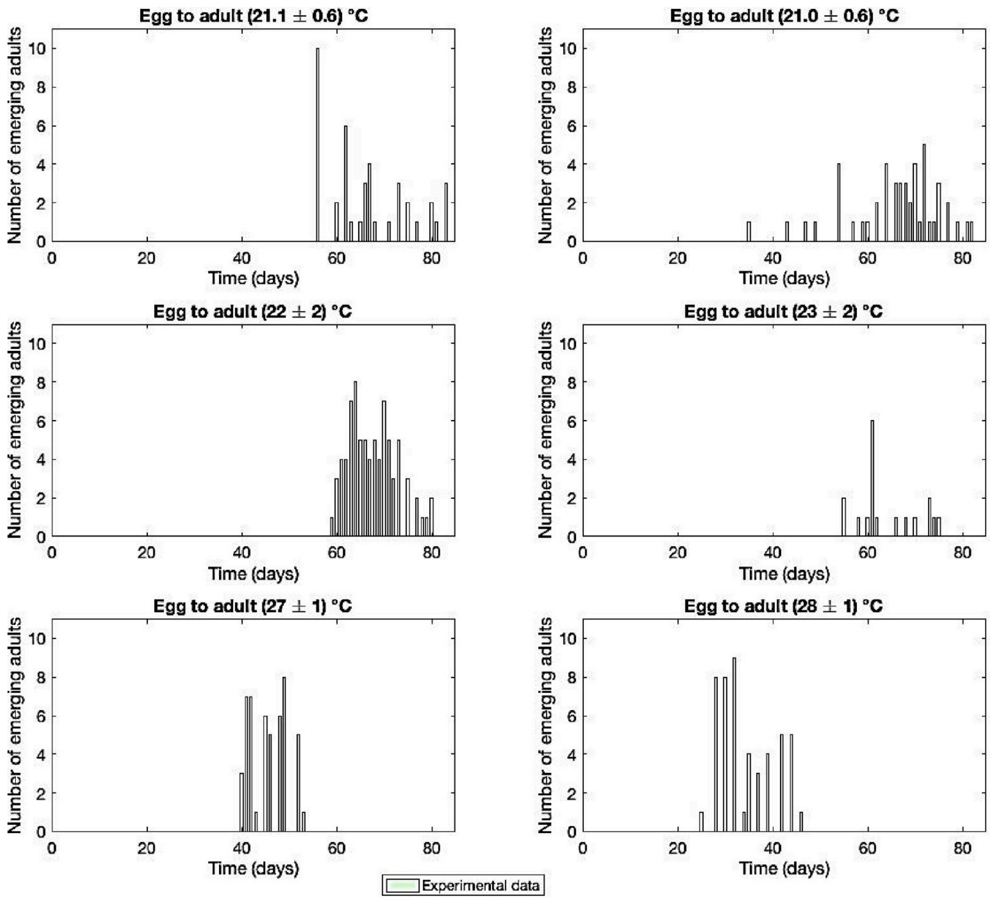

Figure A3.2. General plot of the distribution of the total development time over the different constant temperatures explored in this study.

Appendix 4. Sex-ratio boxplot of emerging BBWs adults over temperatures

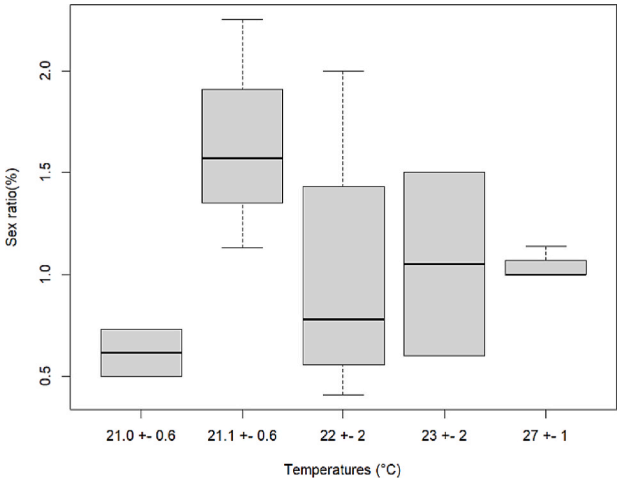

Figure A4. Distribution of the sex ratio over temperature.

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