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The quinoa pest *Copitarsia incommoda* Walker is a cause of significant damage, and it is thus critical for Andean countries to have access to phenological models to maintain production and food safety. These models are key components in pest control strategies in the context of global warming and in the development of sustainable production integrating agroecological concepts. Phenological models are mainly based on outlining the relationship between temperature and development rate. In this study we investigated the combined effect of protein content within the diet (artificial diet; artificial diet with -20% protein; artificial diet with +20% protein; natural quinoa diet) and temperature (12, 16.9, 19.5, 22.7, 24.6°C) as drivers of the development rate. Our study supports the literature, since temperature was found to be the main driver of the development rate. It highlights the significant role played by protein content and its interaction with temperature (significant effects of temperature, diet, and diet:temperature on development time using GLMs for all foraging life stages). We discuss the implications of such drivers of the development rate for implementing and applying phenological models that may benefit from including factors other than temperature. While performance curves such as development rate curves obtained from laboratory experiments are still a useful basis for phenological development, we also discuss the need to take into account the heterogeneity of the insect response to environmental factors. This is critical if pest control practices are to be deployed at the optimal time.

performances | models | nutrition | temperature | development | proteins

Introduction

Insects are ectotherm organisms, so that most phenological models use temperature as their main input variable to represent performances and development rate in particular (Pollard et al. 2020), since performances can be modelled (and pre-dicted) from a knowledge of the temperature experienced by insects (Golizadeh and Zalucki 2012). However, while temperature is the main factor allowing us to build development-rate models (Angilletta et al. 2002), other factors can also be considered, such as photoperiod, as shown in the beet webworm Loxostege sticticalis L. (Lepidoptera: Crambidae) (Kutcherov et al. 2015), or diet, as shown in the red floor beetle Tribolium castaneum Herbst (Lepidoptera: Tenebrionidae) (Scharf et al. 2015). The importance of factors other than temperature and their interactions is nothing new (Uvarov 1931, Lee and Roh 2010), yet these interactions may be more complex than previously appreciated in the literature, notably because of plasticity in life traits (Clissold and Simpson 2015). A study on the gypsy moth Lymantria dispar L. (Lepidoptera: Erebidae), demonstrated that development rate of gypsy moth populations were different depending on the host plant, and that each population had host preferences (Keena and Richards 2020). Even when a single population is considered, the effect of diet is of practical importance as resources can vary significantly in space (eg, crop rotation) and time (eg, plant growth, agricultural practices such as harvest). Another study on the gypsy moth L. dispar showed that the protein:carbohydrate ratio mattered for the species development and growth, with significant development time differences depending on the diet used (Perkovich and Ward 2020).

Here, we focus on the development and survival as a function of temperature and diet of an agricultural insect pest attacking the quinoa crop (Chenopodium quinoa Willd., Chenopodiaceae) in the Bolivian Andes, *Copitarsia incommoda* Walker (Lepidoptera: Noctuidae). Specifically, we focus on protein source content. Protein content was isolated as a single nutritive variable given its fundamental importance in insect development. Proteins are degraded by protease enzymes into amino acids, which are essential components for the production of new proteins, enzymes and tissues. If protein content can be controlled in artificial diets, it is known to vary within plant species and within plant parts (Le Gall and Behmer 2014). Quinoa has gained global interest in recent years due to its nutritional qualities with a balanced composition of amino acids (Repo-Carrasco et al. 2003, Vega-Gálvez et al. 2010), hardiness, and adaptability in the context of cli-

mate change (Ruiz et al. 2014). It is currently cultivated in over 50 countries on all continents and in different ecosystems (Bazile and Baudron 2015). However, most production occurs in the Andes of Bolivia and Peru, covering 80% of international demand (Mujica and Jacobsen 2006). For Bolivia, quinoa constitutes a major crop contributing to food security and exports. It has helped raise the living standards of thousands of families in the highlands in the past decade (Blajos et al. 2014). However, the low fertility of the highland soils and attacks from pests reduce the yield of quinoa and increase production costs. Because of quinoa's strategic importance for the Andean highlands, it is of critical importance to document and predict insect pest phenology if control practices are to be deployed at the right time and production costs for farmers minimized. Among the key insect pests in quinoa are *Copitarsia incommoda* (Walker, 1865) (Lepidoptera: Noctuidae), *Helicoverpa quinoa* Pogue and Harp, 2014 (Lepidoptera: Noctuidae) and *Eurysacca melanocampta* Meyrick, 1917 (Lepidoptera: Gelechiidae) (Cruces et al. 2016, Barrionuevo et al. 2019). This study is focused on *C. incommoda*.

C. incommoda is a polyphagous species that feeds on over 30 crops. It is distributed from Mexico to southern Chile and Argentina, including the Andean mountains of Bolivia and Peru (Angulo and Olivares 2003, Cruces et al. 2016). In Bolivia, it is one of the key pests for quinoa crops due to its larval stage that can cause yield losses of more than 30% (Saravia et al. 2014). *C. incommoda* has six larval stages with coloration varying according to the habitat and organ of the consumed quinoa (Pogue 2011, Cruces et al. 2016). After hatching, small larvae feed on tender leaves, while medium and large larvae consume the quinoa panicle until they complete their development. They pupate on the ground and later emerge as moths, which oviposit between 800 to 1600 eggs in approximately two weeks of life (Choquehuanca Tapia 2011, Gandarillas et al. 2015).

Regarding temperature- and diet-dependent development rates and survival in *C. incommoda*, we expect that in an arid environment like the Bolivian highlands, where resources are limited and temperatures extreme, both factors could be of importance, as well as the interaction between them. We designed an experimental protocol to quantify the importance of each parameter, focusing on their interaction. Accordingly, we address how temperature (five different temperature), diet composition (artificial diet as a control treatment with varying protein content), and the interaction between them affect *C. incommoda* development and survival, and discuss the implication of diet- and temperature-dependences for the characterization of the relationship between temperature and development rate.

Materials and methods

Insect rearing. Rearing of *C. incommoda* and the experiments were carried out in 2018 in the Entomology laboratory of the Kiphakiphani Center (PROINPA Foundation: 16°40´30´´ LS and 68°17´58´´ LO; 3880 m.a.s.l.), La Paz, Bolivia, from a laboratory colony originally collected from quinoa-producing areas in La Paz and Oruro, Bolivia, in 2008 and supplemented with new individuals in 2016 from La Paz department quinoa-producing areas. The larvae from the colony were fed an artificial diet based on quinoa (diet 1 in Table 1), adapted from (Murúa et al. 2003), while adults were fed with a solution of honey and water (1:3). The colony was reared at 21±3°C, 60±5%RH and photoperiod 12:12 (L:D).

Temperatures and diets. To study the effect of diet in interaction with temperature on the development and survival of *C. incommoda*, three artificial diets and one natural diet were used, using an artificial diet as control treatment. The artificial diets were based on a standard diet from (Murúa et al. 2003), adapted by modifying the protein source content. The first diet used an average amount of soya flour and wheat germ (Diet 1, control treatment), with a decrease of 20% for the second diet (Diet 2), and an increase of 20% for the third (Diet 3). The diet compositions are described in Table 1. This artificial diet was originally designed to be able to study *C. incommoda* life cycle under laboratory conditions, and served to characterize the relationship between temperature and development rate (Rebaudo et al. 2017). Quinoa leaves and panicles (the Kurmi variety characterized by a green plant, a pink panicle and white grain) were used for the natural diet, produced continuously in the Kiphakiphani Center greenhouse. The natural diet was solely comprised of the leaves and panicles. Larval stages 1 to 3 were fed with leaves only, while larval stages 4 to 6 were fed with panicles, based on feeding behavior observed in the field (Saravia et al. 2014). The protein content of leaves and panicles (before grain maturation) is estimated to five and nine percent, respectively (Caballero et al. 2015). Breeding environments were established in rearing units at five constant temperatures (12, 16.92, 19.5, 22.68, 24.6°C). Five breeding rooms (3 * 2.5 * 2 m) conditioned at 12±1.2, 16.92±0.9, 19.5±1.6, 22.68±0.7, 24.6±1.3°C (temperature ± standard deviation) and 60±5% RH and 12:12h L:D photoperiod were used. Each room had air conditioning equipment (White-Westinghouse, WAS 09P5AHLW, 1600W), a fan heater (De'Longhi HTF3020, 2000 W) and humidifier (Megafesa 1903 VAPEA, 300W). Throughout the period the temperature and relative humidity of each breeding room were controlled manually every eight hours using a digital thermo-hygrometer (Halthen - TTH 002). The temperature accuracy in each breeding environment was tested in a previous study (Rebaudo et al. 2017) using temperature data loggers (Onset Computer Corporation HOBO TidbiT v2). To contextualize temperatures chosen in this experiment, air outside temperatures in the shade during the quinoa crop growing season from September to April

Ingredients	Diet 1	Diet 2 (-20% proteins)	Diet 3 (+20% proteins)
Wheat germ	27,5 g	24,75 g	30,25 g
Soya flour	27,5 g	24,75 g	30,25 g
Quinoa flake	35 g	35 g	35 g
Baking yeast	20 g	20 g	20 g
Complex B	0,5 ml	0,5 ml	0,5 ml
Ascorbic acid	2 g	2 g	2 g
Potassium sorbate	2 g	2 g	2 g
Methyl paraben	4 g	4 g	4 g
Formaldehyde (40%)	1,5 ml	1,5 ml	1,5 ml
tetracycline	0,5 ml	0,5 ml	0,5 ml
Carrageenan	8,5 g	8,5 g	8,5 g
Water	750 ml	740 ml	755 ml

Table 1. Composition of artificial diets for breeding larvae of *C. incommoda*.

(Winkel et al. 2016) were measured every ten minutes at the Kiphakiphani Center. Average daily temperatures range from 5 to 20°C (with local maximum up to 28°C during the day and a mean daily thermal amplitude of 17°C).

1139 *C. incommoda* eggs of the same age (<12 hours) from 30 pairs of adults were used, which were distributed to 256, 225, 241, 205 and 212 eggs per breeding environment of 12, 16.92, 19.5, 22.68, 24.6°C, respectively, with each individual as a replicate from the same cohort. Eggs were not obtained at the same time so that they could not be systematically distributed across all treatments, but each treatment was based on several females to minimize the maternal effects. Once hatched, the newborn larvae (<12 hours) were individualized in 50 ml plastic rearing containers with 15 cc of artificial diet (based on quinoa) or 15 gr natural diet (quinoa leaves and panicles) and were monitored until they pupated. On the fifth day of pupation they were weighed and sexed based on previous studies in Lepidoptera (Rueda and Ávila 2004, Rondon and Xue 2010), and were then transferred to 10 pairs of pupae per plastic copula cage and oviposition of 3,800 cc (0.15 x 0.15 x 0.2 m) with strips of paper towel (15 x 5 cm) arranged on the inner walls of the cage for egg laying. Once emerged, the adults were fed with a solution of honey and water (1:3) and the eggs in the paper towel strips were removed and placed in Petri dishes (diameter 10 cm and height 2 cm) until hatching.

Data analysis. All data analyses were performed using R version 4.0.3 (R Core Team 2020). From the date of each life stage change, we computed the inverse of the duration of each life stage in days (development rate) for eggs, the six larval stages, prepupa, and pupa, as well as the entire life cycle duration from egg to adult, and the survival rate for each life stage and each temperature. The relationship between temperature and development rate in insects is known to be non-linear, but can be considered as linear in a small range of temperatures (Campbell et al. 1974, Roy et al. 2002, Shi et al. 2015, Sinclair et al. 2016, Quinn 2017, Rebaudo and Rabhi 2018). The temperatures used in this study fall within the zone that can be considered as linear for all life stages of

C. incommoda (Rebaudo et al. 2017). We tested for the relationship between temperature and development rate using simple and polynomial linear models. Then, for each temperature and each life stage, we tested for the effect of diet on development time using general linear models (Poisson family) using the artificial diet as the control treatment, and Tukey tests. We then tested for the effect of diet and temperature on survival rates using a general linear model of the binomial type (link logit), and performed a pairwise comparison of proportions for each diet and each temperature.

Results

Within the range of experimented temperatures, we observed a diminution in the development time as temperature grew, as expected and previously documented for *C. incommoda* (Rebaudo et al. 2017). The relationship between temperature and development rate seemed linear in this range of temperatures (Figure 1A), with the natural diet giving the higher development rate at all experimented temperatures. We also observed a higher variance for higher temperatures (heteroskedasticity), which is expected for insects development rate at extreme temperatures (Couret et al. 2014). The linear models of development rate against temperature demonstrated heteroscedasticity and a pattern in the distribution of residuals, suggesting that we may be at the limit of the linear zone, so we used a polynomial linear model of degree two to adjust to the experimental results (Figure 1B), resulting in a better goodness-of-fit using the Akaike information criterion (eg, AIC of -1624 vs -1471, -1832 vs -1581, -1900 vs -1667, -1860 vs -1597 for the polynomial model vs simple linear model for the total development rate of *C. incommoda* for the four different diets).

Temperature had a significant effect on the development rate for all life stages, as expected and documented in previous studies on the relationship between temperature and development rate. Diet also had a significant effect on development rate except for the egg life stage (F=374.6, df=3, p-value<0.001 for the number of days from egg to adult). When focusing on the three artificial diets, we also observed

no significant effect of the diet on life stage L5 and prepupa, the later corresponding to the shortest life stage with a mean development time of 4.5 days. Interestingly, the interaction between temperature and diet had a significant effect on the development rate (F=4.2, df=3, p-value=0.006 for the number of days from egg to adult). We observed that natural diet allowed a faster development at all temperatures. Also, the artificial diet with less protein negatively affected development, and the diet with additional protein did not confer any significant advantage over the reference artificial diet (Figure 1). When analyzing the development for each life stage, we observed that eggs were not affected by diet (no resource consumption; eggs can be used as a control), and differences were observed from the first larval stage (Table 2). Moreover, we observed that significant differences were detected for the prepupa and pupa life stages (i.e., for life stages without feeding activity), suggesting that the history of larval resource consumption had an effect on following life stages' development rate.

On the range of temperatures used in this experiment, we observed no significant effect of temperature or diet on the survival rate. The pairwise comparison of proportions for each diet and each temperature demonstrated some significant differences between experimental conditions (Figure 2A and Figure 2B), that may be imputed to experimental conditions (overall low survival at 19.5°C).

Discussion

The temperature dependence of development rate in insects has been frequently investigated in the literature (Roy et al. 2002, Quinn 2017, Rebaudo and Rabhi 2018), notably in the context of climate change (Fand et al. 2014, Mwalusepo et al. 2015). Our results support the idea that temperature is the main driver of insect development (Bale et al. 2002), yet our study of *C. incommoda* suggests that nutrition may have a more important role than previously anticipated, especially for studies aiming to predict insect phenology in the face of climate change.

In the laboratory, quinoa crop pests are whenever possible reared using artificial diets (Rebaudo et al. 2017), mostly for convenience, since obtaining fresh material all year long involves access to greenhouses and technical staff to maintain both the insects and plants. However, it has been shown that animals with different developmental histories may respond differently to experimental treatments such as diet (Wiggins et al. 2018). The use of an artificial diet where nutrients may not mirror those available in the field has practical consequences as laboratory-reared individuals may respond differently to field-collected individuals, as exemplified in spiders (Wiggins et al. 2018). Acknowledging this limitation and even if the present study focused in the comparison of artificial diets with variation in the protein content, it revealed that insect development may be faster using natural diet at

all experimented temperatures, as reported for *Drosophila suzukii* (Diptera: Drosophilidae) reared on fruits versus artificial diet (Aly et al. 2016). Not only natural diet can affect development time, but also its quality, as reported for *Plodia interpunctella* (Lepidoptera: Pyralidae) using different natural diets and highlighting the importance of moisture content and the difficulty of representing the variety of food resources available in the insect ecosystem in a performance model (Johnson et al. 1992). Also, different diets can result in significant changes in the life cycle, as shown in *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae) where different numbers of larval instars have been observed as a consequence of diet (Ali and Gaylor 1992). In our case, the observed effect of natural diet may be caused by the presence of natural trace nutrients, or the pest shifts in diet across developmental stage between larval stages 1 to 3 and larval stages 4 to 6 (see Phalnikar et al. 2018). An evaluation of the benefit of using natural over artificial diet would have required to complement artificial diets with natural diets. Also, following results on diet quality in *P. interpunctella* study, by specifically selecting the optimal plant part for each life stage, we can hypothesize that an optimized development could have been obtained.

To add a layer of complexity, insect development rate response to diet may be strain-specific, as demonstrated for *Plutella xylostella* (Lepidoptera: Plutellidae) in a study under laboratory conditions (Carpenter and Bloem 2002). This is all in accordance with a necessary complexity in models making use of development rate performance curves, as acknowledged in the literature (Clissold and Simpson 2015). In our study, we observed an interaction between temperature and diet in the development rate of *C. incommoda*. This may be the consequence of the effect of temperature on food intake, as food intake decrease with growing temperatures, as shown in *Eupterote mollifera* Walker (Lepidoptera: Eupterotidae) (Palanichamy et al. 1982), or in *S. exigua* (Lee and Roh 2010), with direct consequences on development rate, as shown in *Aedes aegypti* Linnaeus (Diptera: Culicidae) (Couret et al. 2014). This could explain the deleterious effect of the diet with a smaller protein content on development rate.

The implication is that models making use of such a performance curve based solely on a single diet might over- or under-estimate development rate, because of the mismatch between available resources in the field and diet in the laboratory. Such an incorrect estimation could however be exceeded by taking into account both i) genetic and environmental variations of individual responses to temperature and diet, for example, plasticity in feeding behavior and foraging activity, or dispersal linked to microclimate selection (Clissold and Simpson 2015), and ii) the spatial and temporal variation in food resources and temperatures (Johnson et al. 1992, Rebaudo et al. 2016, Faye et al. 2017). For the later and as mentioned above, it could be difficult to reproduce in the laboratory the different resources encountered in the fields, as shown in P. interpunctella (Johnson et al. 1992).
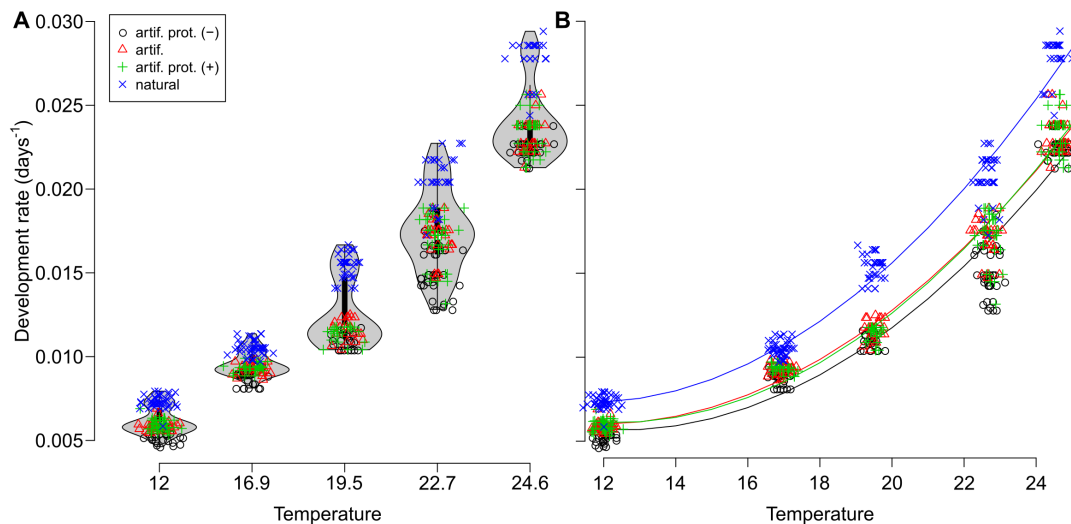
Fig. 1. Development rate at different temperatures for different diets and for total development. Each jittered symbol represents a different diet (black circle: artificial with less protein, red triangle: artificial, green plus: artificial with more protein, blue cross: natural). The violin plots in A were performed using the violin R CRAN package (Adler and Kelly 2019). In B, the lines correspond to a polynomial model of degree two.
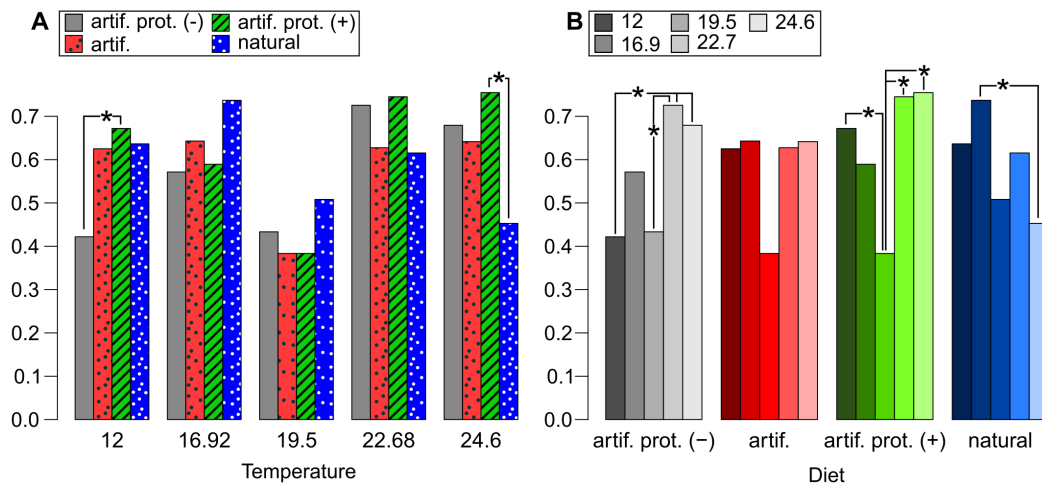

Fig. 2. Survival rate at different temperatures and diets. Each bar represents the proportion of individuals reaching the adult stage. Significant differences are represented with stars in A between diets and in B between temperatures (pairwise comparison of proportions).

The study of *C. incommoda* using different temperatures and diets may suggest another approach, enabling us as to characterize insect temperature-dependent development rate variance and to propose individual-based models integrating such variance in their predictions (Regniere et al. 2012, Chuine and Régnière 2017, Rebaudo and Rabhi 2018).

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	12°C	16.9°C	19.5°C	22.7°C	24.6°C
Egg	0.05±0 (50) a	0.083±0 (50) a	0.143±0 (50) a	0.2±0 (50) a	0.25±0 (50) a
	0.05±0 (50) a	0.083±0 (50) a	0.143±0 (50) a	0.2±0 (50) a	0.25±0 (50) a
	0.05±0 (50) a	0.083±0 (50) a	0.143±0 (50) a	0.2±0 (50) a	0.25±0 (50) a
	0.05±0 (50) a	0.083±0 (50) a	0.143±0 (50) a	0.2±0 (50) a	0.25±0 (50) a
L1	0.035±0.004 (49) c	0.077±0.011 (48) b	0.094±0.012 (49) a	0.143±0.034 (48) c	0.214±0.035 (49) a
	0.053±0.011 (50) a	0.082±0.012 (50) ab	0.098±0.007 (48) a	0.164±0.031 (49) a	0.215±0.045 (50) a
	0.049±0.007 (50) a	0.084±0.013 (50) a	0.097±0.01 (49) a	0.169±0.029 (48) a	0.216±0.046 (50) a
	0.063±0.013 (50) b	0.095±0.008 (50) c	0.14±0.038 (50) b	0.191±0.026 (50) b	0.248±0.012 (50) b
L2	0.087±0.053 (44) b	0.11±0.02 (47) c	0.155±0.04 (48) c	0.21±0.041 (48) b	0.29±0.08 (49) b
	0.117±0.048 (48) ab	0.139±0.03 (50) a	0.255±0.087 (46) a	0.242±0.057 (49) ab	0.336±0.093 (47) ab
	0.131±0.06 (49) a	0.136±0.026 (49) a	0.195±0.076 (47) b	0.251±0.051 (48) a	0.335±0.086 (50) a
	0.128±0.055 (50) a	0.172±0.047 (49) b	0.249±0.063 (49) a	0.423±0.112 (48) c	0.452±0.092 (50) c
L3	0.083±0.023 (40) a	0.105±0.035 (47) ab	0.161±0.044 (48) a	0.183±0.054 (47) c	0.353±0.154 (49) b
	0.103±0.039 (44) a	0.127±0.024 (50) a	0.181±0.062 (46) a	0.222±0.05 (49) a	0.309±0.065 (47) ab
	0.091±0.026 (48) a	0.102±0.021 (49) b	0.178±0.069 (47) a	0.238±0.041 (48) a	0.303±0.072 (49) a
	0.136±0.063 (49) b	0.16±0.077 (48) c	0.246±0.093 (45) b	0.305±0.06 (48) b	0.206±0.037 (48) c
L4	0.088±0.033 (38) a	0.127±0.067 (44) a	0.18±0.068 (46) a	0.178±0.088 (46) c	0.398±0.11 (48) bc
	0.08±0.024 (44) a	0.134±0.032 (49) a	0.186±0.068 (45) a	0.244±0.066 (49) a	0.478±0.076 (47) a
	0.086±0.028 (48) a	0.156±0.07 (49) a	0.164±0.045 (47) a	0.228±0.059 (48) a	0.455±0.184 (44) ab
	0.13±0.061 (49) b	0.136±0.076 (47) a	0.229±0.057 (43) b	0.286±0.056 (47) b	0.373±0.129 (41) c
L5	0.083±0.053 (35) a	0.115±0.032 (42) a	0.17±0.063 (43) a	0.198±0.081 (45) a	0.285±0.082 (48) a
	0.075±0.022 (44) a	0.104±0.049 (49) a	0.152±0.048 (43) a	0.197±0.052 (48) a	0.257±0.06 (45) a
	0.078±0.022 (47) a	0.099±0.027 (49) a	0.164±0.072 (44) a	0.191±0.062 (48) a	0.335±0.109 (44) b
	0.123±0.029 (26) b	0.181±0.071 (19) b	0.234±0.082 (33) b	0.301±0.054 (24) b	0.417±0.115 (23) c
L6	0.082±0.039 (33) b	0.095±0.046 (38) ab	0.077±0.028 (36) a	0.196±0.164 (43) a	0.179±0.073 (45) a
	0.058±0.012 (44) a	0.087±0.027 (47) a	0.085±0.024 (39) a	0.16±0.077 (46) a	0.199±0.048 (42) a
	0.062±0.024 (47) a	0.12±0.064 (48) b	0.082±0.026 (39) a	0.149±0.051 (47) a	0.279±0.107 (41) b
	0.086±0.04 (25) b	0.081±0.02 (19) a	0.129±0.027 (33) b	0.2±0.077 (23) a	0.327±0.131 (23) b
Prepupa	0.18±0.092 (33) a	0.194±0.128 (38) b	0.302±0.113 (30) a	0.273±0.061 (42) b	0.443±0.207 (41) a
	0.153±0.079 (43) a	0.247±0.083 (40) a	0.296±0.106 (31) a	0.293±0.133 (41) ab	0.433±0.128 (40) a
	0.162±0.073 (47) a	0.211±0.072 (42) ab	0.352±0.112 (30) a	0.321±0.17 (42) ab	0.374±0.107 (41) a
	0.157±0.05 (48) a	0.253±0.069 (43) a	0.34±0.065 (40) a	0.346±0.107 (42) a	0.367±0.099 (32) a
Pupa	0.015±0.002 (27) b	0.034±0.006 (32) b	0.034±0.003 (26) a	0.056±0.007 (37) a	0.075±0.007 (36) b
	0.017±0.003 (40) ab	0.031±0.002 (36) a	0.034±0.004 (23) a	0.055±0.007 (32) a	0.071±0.007 (34) ab
	0.018±0.005 (43) a	0.031±0.002 (33) a	0.033±0.002 (23) a	0.055±0.007 (38) a	0.069±0.008 (40) a
	0.021±0.006 (42) c	0.034±0.004 (42) b	0.046±0.005 (31) b	0.056±0.005 (32) a	0.088±0.016 (24) c
Total	0.005±0 (27) c	0.009±0 (32) c	0.011±0 (26) b	0.015±0.001 (37) c	0.023±0.001 (36) b
	0.006±0 (40) a	0.009±0 (36) a	0.012±0.001 (23) a	0.017±0.001 (32) a	0.023±0.001 (34) ab
	0.006±0 (43) a	0.009±0 (33) a	0.011±0 (23) ab	0.017±0.001 (38) a	0.023±0.001 (40) a
	0.007±0 (42) b	0.011±0 (42) b	0.015±0.001 (31) c	0.021±0.001 (32) b	0.028±0.001 (24) c

Table 2. Mean development time and standard deviation at different temperatures and diets. Each line corresponds to a different diet (artificial with less protein, artificial, artificial with more protein, natural), with the number of individuals in parenthesis, followed by the result of a Tukey test (distinct letters within a cell indicate a significant difference in development time).

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