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PAPER

PATHOLOGY/BIOLOGY

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The Effect of Temperature and Laboratory Rearing Conditions on the Development of *Dermestes maculatus* (Coleoptera: Dermestidae)*

ABSTRACT: Experiments were conducted to study the life cycle of *Dermestes maculatus* and to establish the total developmental time and the developmental time of immature stages, in relation with six different temperatures. We also analyzed the variations in size, morphology, and other indicators of temporal variation during life cycle of *D. maculatus*, in relation with temperature. One hundred larvae were selected per experiment, reared individually. The remaining larvae were reared to evaluate and establish temporal variations among the instars (length, cephalic width, and dry weight). In all trials, survivorship was greater than 50% and seven larval instars were found. Data of the average developmental time of immature stages and of the total cycle, at different temperatures, are provided. This is of relevance when estimating particularly, a minimum PMI. No relation between morphometric parameters and temperature was found, suggesting that other random factors may have been involved. Thus, this indicates that the method of isomegalen diagrams could not be used for calculating PMI.

KEYWORDS: forensic science, forensic entomology, cadaveric beetles, controlled conditions, insect development, *Dermestes maculatus*

More recently, *Dermestes maculatus* DeGeer has been recognized as a significant component of the insect fauna associated with decomposing remains, both human and animal. These beetles have forensic significance in helping to estimate the postmortem interval (PMI) (1–6), particularly in cases of advanced decay or skeletonization (7–9), in which they could provide a minimum PMI. In sufficient numbers, they have been reported as reducing a human body to a skeleton in only 24 days (10). Also due to their ability to clear skin and hair off bodies cleanly, *D. maculatus* can be used to clean bones to assist with forensic cases (11). Moreover, dermestids are also relevant in forensic taphonomy as they may also leave macroscopic damage in tissues and bones (9,12). Their presence could also provide evidence of contamination, after exhumation of human remains, during storage in cemetery deposit (13).

The interest for rearing dermestids under laboratory-controlled conditions and in particular for *D. maculatus* arose because of the damage that these insects cause to stored products around the world, including leathers, furs, museum collections, historical materials, poultry farms, and the economical and/or cultural importance that this entails (14–18). The damage is the result of adults and larvae when feeding, as well as by the latter at the moment to pupate (14–18). Furthermore, they are vectors of pebrine, and due to their feeding habits, they can disseminate anthrax (15). Occasionally, they can also cause urticarial and allergic reactions, including rhinitis and asthma (19).

The natural diet of these insects is rich in proteins and lipids, and they are well adapted to a diet with high quantities of fat (20,21). Necrophagous insects strictly require cholesterol or some of its near derivatives. *D. maculatus* do not synthesize polyunsaturated fatty acids, nor do they require them for their normal development (20).

As was mentioned above, it is important to study their biology under certain rearing conditions due to their relation with cadavers, in order to increase the basic knowledge to perform entomological forensic examinations. To this date, only one work has provided some information on the development of *D. maculatus* at different temperatures (22). Moreover, the sample size and the number and range of temperatures used in that study were different to those evaluated in this work.

The aims of this work were to study the life cycle of *D. maculatus* in Argentina and to establish the length of total development and of the immature stages, in relation with different temperatures, as well as to analyze the variations in size, morphology, or other indicators of temporal variation during the life cycle of *D. maculatus*, also in relation with temperature.

Materials and Methods

Establishment of a Colony

The culture of *D. maculatus* was started in 2010 at the Departamento de Biología, Bioquímica y Farmacia vivarium, Universidad

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Nacional del Sur, Bahía Blanca, Argentina. This was possible by collecting adults from decomposition and succession experiments (23). The culture was maintained at 25 ± 3°C, 54 ± 5% relative humidity, and 12:12 h L:D photoperiod. Sand and a piece of cotton were placed as substrates and to provide refuge for the beetles. As a water source, the piece of cotton was soaked with distilled water. Pieces of soft wood of aged poplars (*Populus alba*) were also added to provide alternative refuge for the insects and place to pupate. Insects were fed with beef with or without bone, boiled during 10 min to minimize colonization by fungi, mites, and other pathogens. Containers were cleaned when ammonium or humidity became concentrated.

Rearing D. maculatus *at Different Temperatures*

The temperatures were established after calculating the average maximum temperatures of the last 10 years for the city, taking into account the average of the most representative months per season: 24°C (October and November, spring), 30°C (January and February, summer), 20°C (April and May, Fall), and 15°C (June and July, winter). We also studied intermediate mean temperatures (27 and 22°C) to those calculated for the spring and summer, and spring and autumn, to register what happens at a higher or lower temperature, respectively, for each season.

We obtained pupae from the colony and sexed them (24). Eighteen adults were selected (nine of each sex) and distributed among three plastic containers of 10 cm length × 8 cm diameter, three couples per container. As in the colony, we added 3 cm of sand and pieces of distilled water-soaked cotton to provide refuge and a source of water. The insects were fed with approximately 3 g of the same kind of meat that was used for the colony, weighted using a scale (Acculab 333, Bradford, MA).

The containers were introduced in an incubator (Obsar, Córdoba, Cba) for invertebrates at the temperature to be evaluated (±0.1°C), 55.4 ± 2% relative humidity, and 12/12-h light/dark photoperiod. The containers were inspected daily to collect and quantify eggs. These were placed into other plastic containers to record hatching, which also required daily observations. When this happened, 100 larvae were selected and their development was also followed daily until adult stage, to assess the total length of development and the length of each stage (molting, survivorship, and morphological characters were checked). Each larva was placed in a container 3 cm length × 1.5 cm diameter and fed with the same type of food given to adults (0.8 ± 0.2 g). As in the colony, a piece of soft wood provided the larva refuge and place to pupate. The remaining larvae were reared as a group to evaluate and establish temporal variations among the instars (length, cephalic width, and dry weight), for which 20 specimens of each instar were randomly extracted (except when the number of individuals that molted to an advanced specific instar was smaller than that established), killed, and preserved in ethanol 70%. The larval body length was measured from the rearmost abdominal segment to the clypeus, excluding mandibles, using a stereoscopic microscope (Zeiss Stemi SV6, Scotts Valley, CA) with micrometer oculars. Pupae were measured from the head to the rearmost abdominal segment with a piece of millimeter paper. The samples from each experiment were weighted with an analytic digital scale (Shimadzu L200, São Paulo, SP), after drying them at ambient temperature for 48 h. The new pupae were sexed to obtain virgin adults for further assays.

Statistical Analyses

Results are expressed as minimum (Min), maximum (Max), and mean ± standard error (SE). The number of survivors during all the experiments and from each larval instar and pupal stage was evaluated. In this case, we also considered a replicate obtained at 30°C (30r), so that seven trials were involved.

In each trial, the developmental time of each larval instar and pupal stage was established following the development of each specimen. The prepupal period was not separated from the last larval instar.

Kruskal–Wallis tests and pairwise comparisons were carried out following Conover (25) to evaluate whether the developmental time of the different stages, larval instars, and total cycle was affected by temperature. In the case of larval instars, after applying the test mentioned above, a contrast was performed to evaluate linear tendency between temperatures for each larval instar.

To analyze morphometric parameters of larvae, we used the instars with $n = 20$ specimens. A model was adjusted depending on the parameters studied. The resultant straight lines were compared by analysis of covariance (ANCOVA). When factors other than temperature were suspected to be affecting or making changes in the interception point, these were considered random factors. Thus, a common equation was estimated, taking into account the ANCOVA results. We also evaluated whether the length of pupae changed with temperature using Kruskal–Wallis test and pairwise comparisons (25).

All statistical analyses were carried out using InfoStat (version 2011) FCA—Universidad Nacional de Córdoba (Argentina).

Results

Embryonic Development

Eggs were deposited in the sandy substrate, adhered to cotton fibers or to small stones in the sand. As embryonic development progressed, rows of large curved brown-reddish setae appeared from the posterior to the anterior end of the body, and that coloration became deeper as the moment of hatching approached, when ocelli appeared at each side.

The mean developmental time needed as egg decreased as temperature increased ($p < 0.05$) (Table 1).

Postembryonic Development: Larval Cycle

Larvae used different substrates and materials not only as refuge but also to pupate, among them sand, cotton, wood, and cadaveric tissue. The transformation from pupa to adult stage could be discerned because changes occurred in coloration: mandibles, nails, and legs became a brown color, followed by the wings and head. Finally, the hair on the wings became

TABLE 1—*Developmental time for egg of* D. maculatus *at different constant temperatures.*

	Developmental Time (Days)			
Temperature (°C ± 0.1°C)	Min	Mean	Max	*n*
15	5	9.7	13	100
20	5	5.8	6	100
22	3	4.7	6	100
24	2	3.8	5	100
27	2	3	3	100
30	2	2.3	3	100

darker and more abundant, and the abdominal marking characteristics of the species appeared.

Seven instars were observed at all temperatures (L1–L7), with an additional eighth instar (L8) recorded at 20 ± 0.1°C.

The developmental time of each larval instar (L1–L8) decreased at higher temperatures ($p < 0.01$) (Table 2).

When the relations length–cephalic width, length–weight, length–instar, and weight–instar were studied, the ANCOVA results showed that there was not a clear pattern in relation to temperature, and that other factors could probably determine the changes in the point of interception. In all of these relations, we found that temperature had statistically parallel but not coincident adjustments, except in the first temperature, where they were coincident. We observed that at more advanced larval instars, the length and weight of individuals was greater (Fig. 1). Furthermore, at a greater length, the weight and cephalic width of the larvae increased as well.

In all the experiments, we found that as time progressed, the size and weight of the larvae increased. Through the ANCOVA results, we found that at low temperatures, the growth in length was slower (0.13 mm/day) than that of intermediate (0.34 mm/day) and higher (0.61 mm/day) temperatures ($p < 0.05$) (Fig. 2); similar results were obtained for the speed of weight gain, which was slower at low temperatures (0.08 g/day) than at intermediate (0.165 and 0.24 g/day) and higher (0.39 g/day) temperatures ($p < 0.05$).

Postembryonic Development: Pupa

The developmental time of the pupal stage showed significant differences across temperatures ($p < 0.05$) (Table 3). Thus, at higher temperatures, the pupal stage was shorter. The analysis of body length showed that at 15 ± 0.1°C and 20 ± 0.1°C, pupae were shorter than those reared at the other temperatures ($p < 0.05$).

Total Development

The total survivorship in all experiments was greater than 50% (Table 4). Mortality was attributed to arrested molting or fungal infections, although in some instances, there was not an apparent reason. We could not detect a clear relationship between survivorship and temperature. However, it should be noted that the lowest temperature studied which showed 55% of survivors corresponded to an extreme temperature (15°C). Survivorship at the rest of the temperatures fluctuated between 63% and 98%, with an average of 80%.

When all the survivors from L1 to pupa were considered (Fig. 3), the greatest mortality corresponded to L2 (31.9%) followed by L1 (21.5%).

Finally, we found that at a greater temperature, the developmental time of the total cycle was shortened ($p < 0.05$) (Table 5).

Discussion

A *D. maculatus* colony could successfully be established under the laboratory conditions assessed. This also allowed performing studies on the biology of this species and the other aims proposed in the present work.

Contrary to other authors who found eggs in the feeding substrate (26,27), we observed them in the sandy substrate under the food or in farther areas, or adhered to the cotton fibers or to

TABLE 2—*Developmental time for each larval instar and for the total larval stage of* D. maculatus *per temperature.*

Temperature (°C ± 0.1°C)	Developmental Time of Each Larval Instar (Days, Mean ± SE)								Total Larval Developmental Time (Days, Mean ± SE)
	L1	L2	L3	L4	L5	L6	L7	L8	
15	12.2 ± 0.30 ($n = 82$)	12.9 ± 0.38 ($n = 71$)	10.7 ± 0.29 ($n = 68$)	10.4 ± 0.27 ($n = 67$)	12.3 ± 0.68 ($n = 64$)	23.9 ± 1.33 ($n = 53$)	29.9 ± 1.04 ($n = 16$)	0 ($n = 0$)	85.6 ± 1.59 ($n = 64$)
20	5.1 ± 0.10 ($n = 96$)	6.9 ± 0.20 ($n = 85$)	7.2 ± 0.22 ($n = 83$)	7.8 ± 0.16 ($n = 82$)	14.6 ± 0.78 ($n = 79$)	20.3 ± 0.93 ($n = 40$)	17 ± 2.94 ($n = 4$)	21 ($n = 1$)	52.7 ± 1.14 ($n = 77$)
22	4.6 ± 0.09 ($n = 100$)	4.8 ± 0.09 ($n = 100$)	5 ± 0.09 ($n = 100$)	4.6 ± 0.1 ($n = 99$)	6.9 ± 0.4 ($n = 99$)	14.2 ± 0.28 ($n = 80$)	14.8 ± 0.25 ($n = 4$)	0 ($n = 0$)	37.9 ± 0.39 ($n = 98$)
24	3.8 ± 0.05 ($n = 95$)	3.9 ± 0.09 ($n = 89$)	3.2 ± 0.09 ($n = 81$)	4.1 ± 0.10 ($n = 79$)	9.0 ± 0.55 ($n = 74$)	12.5 ± 0.61 ($n = 28$)	15 ($n = 1$)	0 ($n = 0$)	29.2 ± 0.52 ($n = 71$)
27	2.9 ± 0.07 ($n = 97$)	3.4 ± 0.11 ($n = 84$)	3.6 ± 0.09 ($n = 73$)	3.3 ± 0.11 ($n = 67$)	4.9 ± 0.23 ($n = 65$)	9.3 ± 0.30 ($n = 57$)	9.6 ± 0.32 ($n = 8$)	0 ($n = 0$)	27.7 ± 0.43 ($n = 63$)
30	2.9 ± 0.07 ($n = 96$)	2.3 ± 0.07 ($n = 85$)	2.1 ± 0.06 ($n = 84$)	2.6 ± 0.07 ($n = 84$)	5.3 ± 0.29 ($n = 84$)	7.0 ± 0.19 ($n = 41$)	7 ($n = 1$)	0 ($n = 0$)	18.7 ± 0.19 ($n = 84$)
H Estadistic	427.24*	400.81*	386.74*	384.66*	159.50*	178.67*	7.31*	–	404.02*

*$p < 0.01$.

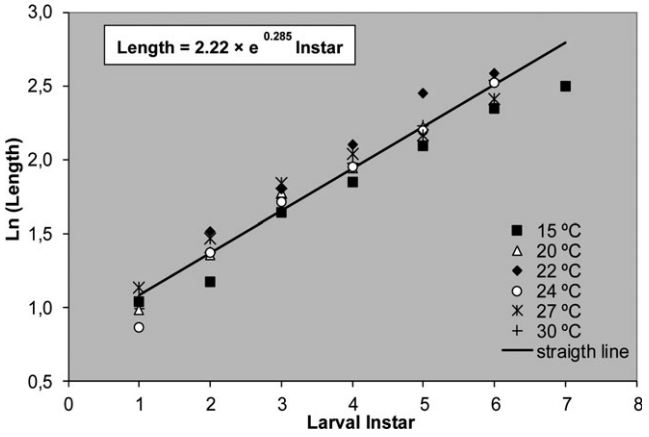

FIG. 1—*Relation between larval instar and length (mm) at different temperatures.*

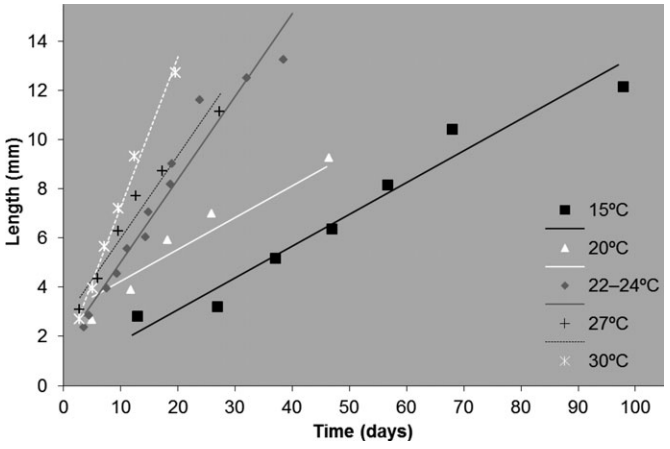

FIG. 2—*Relation between time and length at different temperatures.*

TABLE 3—*Developmental time for pupal stage of* D. maculatus *at different constant temperatures.*

	Developmental Time of Pupa (Days)			
Temperature (°C ± 0.1°C)	Min	Mean	Max	*n*
15	12	14.5	20	55
20	11	15.1	17	77
22	8	12.9	14	98
24	8	10.4	12	71
27	7	7.7	8	63
30	3	6.3	10	84

TABLE 4—*Total survival for postembryonic development of* D. maculatus *per temperature.*

Temperature (°C ± 0.1°C)	% of Survival
15	55
20	77
22	98
24	71
27	63
30	84
30r	89

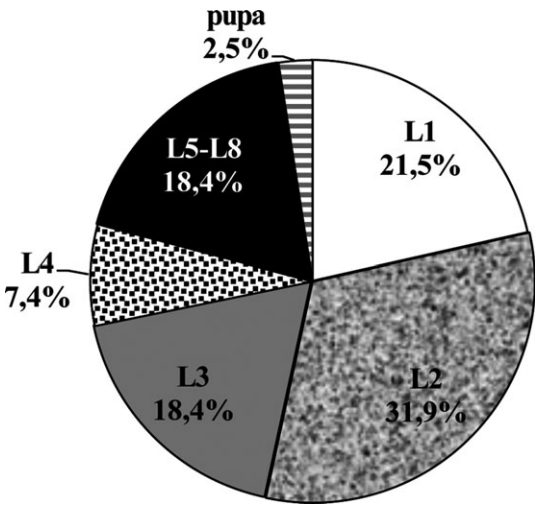

FIG. 3—*Mortality of larval instars and pupal stage.*

TABLE 5—*Total developmental time of* D. maculatus *at different temperatures.*

	Total Developmental Time (Days)			
Temperatures (°C ± 0.1°C)	Min	Mean	Max	*n*
15	106	114	128	55
20	61	73.7	99	77
22	41	55	70	98
24	35	43.4	57	71
27	32	38.3	46	63
30	23	27.3	34	84

small stones in the sand. This could be related to the diverse materials which were provided, and it is an important clue to consider at a crime or cadaver finding scene when collecting entomological evidence. The characteristics observed during the embryonic development in this study matched those reported by Ede and Rogers (28). We observed that the mean embryonic developmental time decreased with increasing temperature, a trend that was also found in some studies with dipterans (29,30). The mean embryonic developmental time that we observed was of 2.3 ± 0.05 days (55.2 h) at 30°C ± 0.1°C, 3.8 ± 0.08 days at 24°C ± 0.1°C, and 5.8 ± days at 20°C ± 0.1°C. Other authors reported a mean incubation period of 44.5 h at 29°C ± 2°C (31), 3.4 ± 0.5 days at 24.15°C ± 0.95°C (32), and 6.7 days at 20°C (33). The longer embryonic developmental time found in our study with respect to others reports could be attributed to the diet used to feed adults. In fact, other authors reported changes in the larval developmental time, which were attributed to the high levels of cholesterol and proteins in the food (34).

We found seven larval instars in all the trials, as well as an additional eighth instar at 20 ± 0.1°C. As reported by Hinton (15), *D. maculatus* normally molts six times before pupating, but it can molt up to eleven times. Taylor (35) mentioned between six and ten larval instars, PisfH and Korytkowski (32) observed six, Osuji (36) reported between five and seven, and Ezenwaji and Obayi (37) recorded five instars. Thus, the forensic entomologist must have care when estimating PMI or providing information in a forensic context. The intraspecific variation in nymphal and larval instars is a widely distributed phenomenon among hemimetabolic and holometabolic insects. Several factors can affect the number of instars, particularly temperature (38), photoperiod (39), quantity

and quality of the diet (40), humidity (41), density (42), diapause (43), presence of lesions (44), genetics (45), and gender (46). Furthermore, these variables can interact among them (47). However, invariability in the number of larval instars is considered as "normal," and no importance has ever been given to the issue (48).

We could not establish a clear relation between the morphometric parameters and temperature. This is important to consider because indicates that the method of isomegalen diagrams would not be appropriate to calculate PMI. Considering that humidity, photoperiod, food, substrates, containers, and population density were also controlled, we conclude that other random factors could have been involved. For example, using offspring from different populations for the different experiments, and/or that trials were conducted at different times, could have influenced the outcome. Genetic differences between populations may also be affecting these results. Thus, conducting experiments on offspring from parents reared in the laboratory for generations may sometimes be disadvantageous, as expressed by Wagner et al. (49). We found that at a greater body length, the larvae were heavier and also exhibited greater cephalic width. Furthermore, at more advanced larval instars, the length and weight of individuals increased. Ezenwaji and Obayi (37) observed the same relation between length and larval instars. It could be adaptive for these beetles to go through more larval instars when the growth rates are high (favorable environmental conditions), because it could be advantageous to have a large size at a relative low cost (low mortality). Body size has often been shown to be positively correlated with various aspects of fitness (50–52). This could be related to the fact that at a greater body size, performance and dominance of organisms or fitness increase (53,54). In terms of evolution, this means that directional selection favors the increase in size of organisms of many natural populations, although this could result in costs and important risks. Furthermore, genetics differences in lineages can have different reaction norms for a particular environmental variable, as shown for *Drosophila* lineages (55). Genetic changes in size can also occur as a result of an artificial active selection.

Predictably, we found that as time progressed, the size and weight of the larvae increased. Roff (56) proposed that the development of a big body needs a greater time for development. Other works with dipterans established that the length of larvae increased as a function of time (30). We found through ANCOVA that the speed of growth in length and weight gain of larvae increased at higher temperatures. Increasing rearing temperatures generally increases the development and growth rates and so favorably shortens the development time (time to adult or reproduction) (57,58). The vulnerability of individuals is thus reduced by shortening the time of exposure to enemies, which increases the chances of successful mating and reproduction of adults as suggested by Blanckenhorn (50).

The differences found in the length of larval and pupal periods in comparison with other reports could be attributed to food, humidity of food, relative humidity (15,36), as well as genetic variations between individuals and populations due to geographic variations (59). This has to be taken into account when evaluating forensic cases and information of other works is used as reference.

The developmental time of *D. maculatus*, from egg to adult, was inversely related to temperature. This same phenomenon was found by Richardson and Goff (22). As mentioned above, general consensus establishes that with increasing rearing temperatures, the development and growth rates are increased, and therefore, the development time is shortened (time to adult or reproduction) (57,58). Differences in developmental time found between this work and others at similar temperatures could be due to the same causes mentioned before for the larval and pupal periods.

As reported by Richardson and Goff (22), the survivorship from egg to adult was positively correlated with temperature. Moreover, they mentioned that the temperatures 25, 30, and 35 (±2°C) resulted in lower mortality. Majeed (60) found that larval survivorship decreased with an increase in temperature. Nonetheless, our results did not show a clear relationship between temperature and survivorship, although a greater number of specimens were used. Richardson and Goff (22) suggested that the first larval instar could be more susceptible to the effects of temperature; moreover, they mentioned that at 30°C, the mortality during that instar was higher, and at 35°C, it reached 100%. However, the number of deaths we recorded at the first larval instar was low (25%). We found that in all trials, the general survivorship was greater than 50%. The lowest survivorship corresponded to 15°C, which could indicate that this temperature could be the greatest of the unfavorable temperatures for the life cycle of *D. maculatus*. Richardson and Goff (22) found that no larvae completed development at that temperature and in general in the other trials the survivorship was not high. Our findings could suggest that the rearing protocol that we used could be applied by other researchers when carrying out studies or forensic cases.

Finally, these data could be of relevance when estimating PMI and other parameters related to forensic entomology of *D. maculatus*. Moreover, information in literature is scarce regarding factors that affect variability and on which physiological mechanisms may be involved. Future studies should further explore such mechanisms.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relation between cephalic width and length of the larvae at different temperatures.

Figure S2. Relation between length (mm) and weight (μg) of the larvae at different temperatures.

Figure S3. Relation between larval instar and weight (μg) at different temperatures.

Figure S4. Relation between time and weight (μg) at different temperatures.

Table S1. Estimation (±SE) of the parameters (α = interception point; β = gradient) of the transformed equations of the relations: length–weight of larvae, length-cephalic width of larvae, length-larval instar, weight-larval instar, for all temperatures.

Table S2A. Length (mm) of each larval instar and pupa at each temperature.

Table S2B. Cephalic width (mm) of each larval instar at each temperature.

Table S2C. Mean weight (μg) of each larval instar at each temperature. L7 and L8 were not included because the weight of the individuals was not registered.

Table S3. Estimation (±SE) of the parameters (α = interception point; β = gradient) of the transformed equations of the relation length-time since ANCOVA results.

Table S4. Estimation (±SE) of the parameters (α = interception point; β = gradient) of the transformed equations of the relation weight-time since ANCOVA results.