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Biological Strategies of *Dermestes maculatus* DeGeer (Coleoptera: Dermestidae) at Larval Stages in Different Temperatures

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Abstract

The intraspecific variation in larval instars is a widely distributed phenomenon amongst holometabolous insects. Several factors can affect the number of instars, such as temperature, humidity, and density. Only a few references could be found in the literature because the invariability in the number of larval instars is considered normal, and the issue has raised little to no interest. Despite this, no study to date has intended to assess or focus on the larval development. Here, we analyzed the effect of different rearing temperature on the larval stage of *Dermestes maculatus* DeGeer (Coleoptera: Dermestidae). The results indicated that at all temperatures, L5 represented a decisive point for individuals as well as the other later larval instars, because the next step to follow was to pupate or molt to the next larval instar. Furthermore, there were mainly two populations, L5 and L6, although in different proportions according to temperature. We also found that at a greater number of instars, the larval development at all temperatures lasted longer. Moreover, the exponential model was the best adjustment in the developmental time of all populations as well as for the accumulated developmental time of L1–L4. Thus, we conclude that random factors such as genetics could probably cause interspecific variability in *D. maculatus* larval development.

Introduction

Holometabolous insects are known to molt regularly during their development, and the larval stage can be divided into instars (period between two successive molts). To this date, it is hard to tell whether some taxa are more prone than others to display intraspecific variability in the number of instars (Esperk *et al* 2007).

The interest for rearing dermestids under laboratory controlled conditions and in particular for *Dermestes maculatus* DeGeer (Coleoptera: Dermestidae) arose from different needs. It is also important to study their biology under certain rearing conditions due to their relation with cadavers and so to increase both basic knowledge and entomological expertise.

Some authors that perform studies with *D. maculatus* mentioned that this species can molt five or more times before pupating. Hinton (1945) reported that these beetles normally molt six times before pupating, but they can molt up to 11 times; Taylor (1964) mentioned between 6 and 10 larval instars, Vidal Sarmiento & Alzuet (1965) observed 11; PisfH & Korytkowski (1974) recorded six, Osuji (1975) and Haines & Rees (1989) reported between 5 and 7, Ezenwaji & Obayi (2004) mentioned five, Zakka *et al* (2013) observed six molts, and Zanetti (2013) and Zanetti *et al* (2015) recorded principally between 5 and 7 instars.

The intraspecific variation in larval instars is a widely distributed phenomenon amongst holometabolous insects. Several factors can affect the number of instars, particularly

environmental factors such as temperature, photoperiod, quality and quantity of food, rearing density, and humidity (Esperk *et al* 2007). Aside from environmental factors, the presence of lesions, sex and inheritance, can also influence the number of instars (Esperk *et al* 2007). Only a few references could be found in the literature because the invariability in the number of larval instars is considered normal, and the issue has raised little to no interest (Esperk *et al* 2007). Because of the results obtained in a previous study on the life cycle of *D. maculatus*, as well as the reasons mentioned above, the aims of the current research were to study and characterize the larval development of *D. maculatus*, in relation with different temperatures characteristic of each season and intermediate of spring and summer and spring and autumn, for a semirural area of Bahía Blanca, Argentina.

Materials and Methods

Rearing at different temperatures

To perform these experiments, we sexed pupae (Halstead 1963) from a previously established colony. Eighteen adults were selected (nine of each sex) and distributed among three plastic containers, three couples per container. We added 3 cm of sand and pieces of cotton, which provided a refuge, and a source of water when these were sprayed with distilled water. Approximately 3 g of boiled beef was added after being weighted using a precision scale (Acculab 333, Bradford, USA).

The containers were introduced in an incubator for invertebrates (Obsar THR, Córdoba, Argentina) at 15, 20, 22, 24, 27, and 30°C ($\pm 0.1^\circ\text{C}$), 55.4 \pm 2% relative humidity, and 12-/12-h light/dark photoperiod. The temperatures were determined as described in Zanetti (2013) and Zanetti *et al* (2015). For each temperature, the cultures were inspected daily to collect and quantify eggs. These were removed and placed in different plastic containers to register hatching, which also involved daily observations. When this happened, 100 larvae were selected and their development was also followed daily until adult stage, in order to record the developmental time of each stage and of the total cycle. Each larva was placed in a container 1.5-cm diameter \times 3 cm high and fed 0.8 \pm 0.2 g of boiled beef. Sand and a piece of cotton were placed into the container with the same purposes as for adults, as well as a piece of soft wood to provide the larva another refuge and place to pupate. The new pupae were sexed in order to have virgin adults for further experiments.

Statistical analysis

In each experiment, the developmental time per larval instar and pupal stage was established following the development

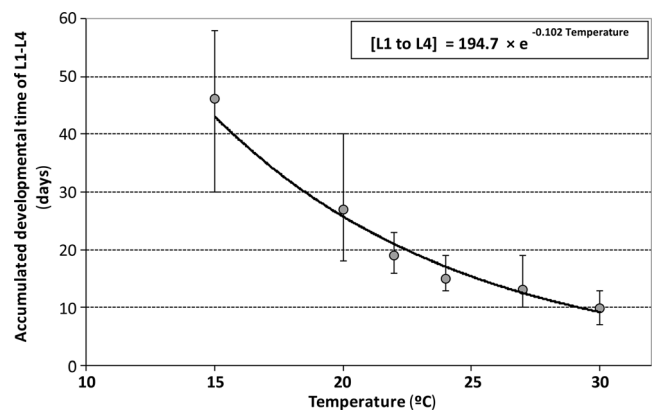


Fig 1 Mean accumulated developmental time of L1–L4 in function of temperature.

of each specimen. The prepupal period was not separated from the last larval instar.

To visualize the way in which larvae were distributed along their cycle, and to detect possible behaviors resulting from different strategies, they were ordered from shorter to longer total developmental time, placing first those which had the fifth (L5) instar as the last, then those which finished at the sixth (L6), seventh (L7), and eighth (L8) instars (only for those completing the cycle to adulthood). A replicate obtained at 30°C (30r) was included when we studied whether temperature determined the last larval instar, so seven experiments ($n = 700$) were involved.

The total larval developmental time as a function of the last instar until to pupate per temperature was evaluated through the Kruskal-Wallis test, and pair comparisons were made following Conover (1980). These tests were also performed to make other comparisons of interest.

To study the accumulated means of the developmental time of the first fourth instars (L1–L4) as a function of temperature, as well as the means of the total larval developmental time as a function of temperature considering the last larval instar before pupating (population), we adjusted different models (all of them with no more than two parameters).

All statistical analyses were conducted using Info Stat (version 2011) FCA, Universidad Nacional de Córdoba (Argentina).

Table 1 Estimation (\pm SE) of the parameters of the transformed equations since ANCOVA results.

Larval instar	Parameters	Estimation	SE
L1 to L4	α	5.2715	0.0324
	β	-0.1019	0.0014

Table 2 Accumulated developmental time (days) for L1–L4 of *Dermestes maculatus* during each temperature.

Temperature (°C ± 0.1°C)	Min	Media	Max	n
15	30	46.09	58	67
20	18	26.88	40	82
22	16	19.00	23	99
24	13	14.92	19	79
27	10	13.12	19	67
30	7	9.94	13	84

Results

When the effect of temperature on the developmental time of L1–L4 was evaluated, we found a decrease in the accumulated developmental time as temperature increased (Fig 1; Table 1). This tendency was not linear but was adjusted to an exponential model following the equation:

$$[L1 \text{ to } L4] = k \times e^{\beta \text{Temperature}}$$

where *k* is the scale parameter, *e* is exponential, and β is the shape parameter. With the exponential model, not only the evident curvature was corrected but also the marked heterocedasticity.

Contrary to the unimodal behavior exhibited by the first four larval stages, we observed that L5 represented a decisive point for individuals, because the next step to follow was either to pupate or to molt to the next larval instar. The same happened with the later instars L6, L7, and L8. Tables 2 and 3 show the descriptive statistics for the accumulated developmental times of L1–L4 and for the total larval developmental time, considering the last larval instar before pupa (L5, L6, L7, and L8), respectively.

We did not detect a clear pattern between larval strategy (last larval instar) and temperature (Fig 2). Therefore, other factors could determine the last larval instar prior to pupating. Since we found different strategies that an individual

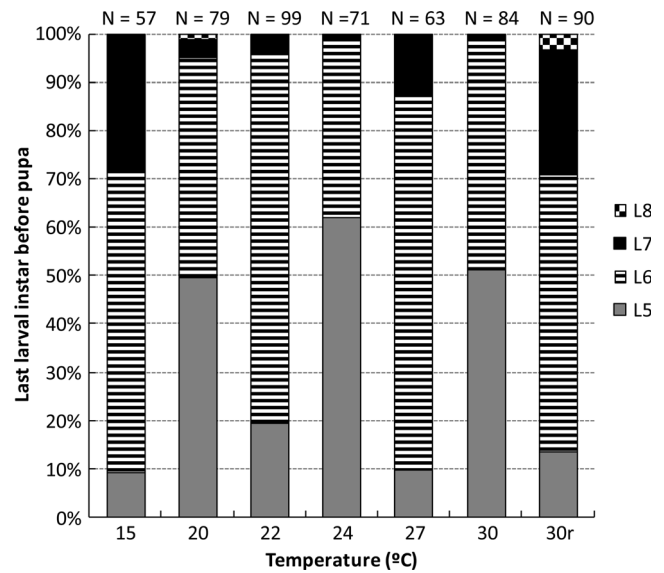


Fig 2 Last larval instar before pupating, per experiment.

may follow after L5 leads us to suspect the existence of various statistical populations. At all temperatures, there were mainly two populations, L5 and L6 (Fig 3), although in different proportions and abundances (Fig 2). In four of them, most larvae pupated at L6 (15 ± 0.1°C, 22 ± 0.1°C, 27 ± 0.1°C, and 30r), whereas less than 20% pupated at L5. In the other three, the proportion oscillated slightly in favor of L5 (20 ± 0.1, 24 ± 0.1, and 30 ± 0.1°C), with ca. 50% of the larvae pupating at L6. A third population, L7, could be distinguished, particularly at 15 ± 0.1°C, 27 ± 0.1°C, and 30r.

Out of 700 individuals, 537 reached the adult stage, indicating a high survivorship (76.7%). Figure 4 shows a schematic of the survivors and dead individuals during post-embryonic development. It can also be seen how many of the survivors molted to the next larval instar or pupated. The individuals able to molt from one instar to the next were greater than 90%. From L5, this percentage decreased because, as mentioned before, it depended on whether the larva pupated (29.42% L5 (N=571); 80.88% L6 (N=387);

Table 3 Total larval development time (days) of *Dermestes maculatus* considering the last larval instar.

Temperature (°C ± 0.1°C)	Instar															
	L5 to pupa				L6 to pupa				L7 to pupa				L8 to pupa			
	Min	Media	Max	n	Min	Media	Max	n	Min	Media	Max	n	Min	Media	Max	n
15	84	86.80	93	5	77	86.40	98	35	91	97.88	107	16				
20	39	46.53	72	38	42	57.03	71	35	69	73	80	3	77	77	77	1
22	30	33.42	45	19	35	38.63	46	76	46	47.75	49	4				
24	23	27.11	42	44	28	32.19	39	26	41	41	41	1				
27	21	23.17	26	6	21	27.24	35	49	29	33.50	35	8				
30	15	17.91	22	43	15	19.53	25	40	20	20	20	1				

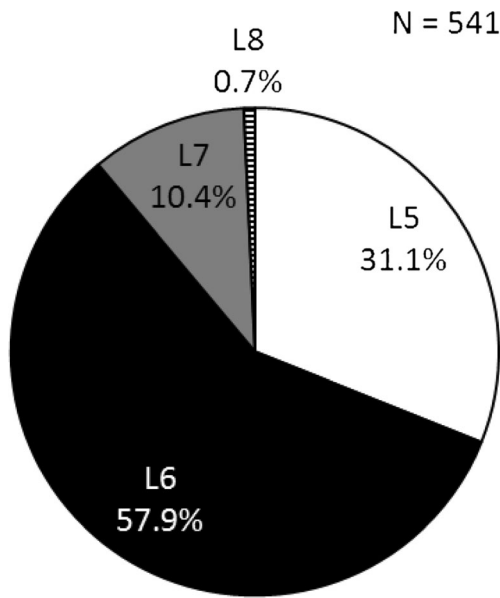


Fig 3 Last larval instars (populations).

88.89% L7 ($N=63$) or molted to the following larval instar (67.78% L5 ($N=571$); 16.28% L6 ($N=387$); 6.35% L7 ($N=63$)); the remainder percentages corresponded to dead larvae.

In Table 4, we provide the descriptive statistics for the larval instars when individuals molted to either the next instar or to pupa. Some differences can be observed on the developmental time of instars across temperatures ($P < 0.05$), depending on the strategy followed by individuals. In all the experiments, the developmental time of the larval instar which molted to pupa was greater than that which molted to the next larval instar ($P < 0.05$). In general, we found that at a greater number of instars before pupa, the total larval developmental time was longer at all temperatures ($P < 0.05$). There were no significant differences in the developmental time of the last larval instar before pupating between statistical populations ($P < 0.05$).

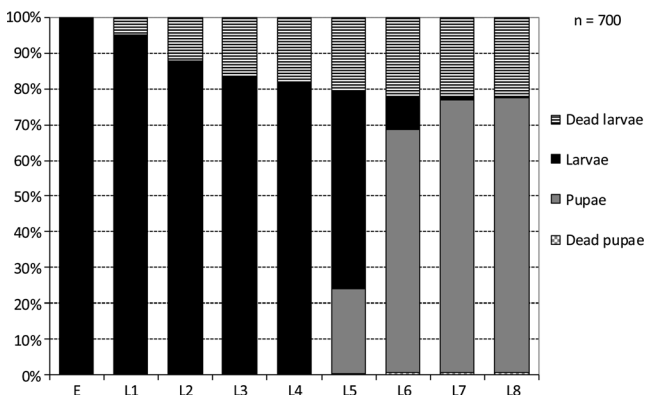


Fig 4 Survival, mortality, and molting of all individuals through post-embryonic development.

Table 4 Developmental time (days) for last larval instars of *Dermestes maculatus* considering the individuals that molted to the next instar and that which molted to pupa.

Temperature ($^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$)	15				20				22				24				27				30			
	Min	Media	Max	n	Min	Media	Max	n	Min	Media	Max	n	Min	Media	Max	n	Min	Media	Max	n	Min	Media	Max	n
L5	7	10.8	15	59	6	8.73	12	40	4	5.10	7	80	3	4.27	6	30	2	4.36	6	59	1	2.76	4	41
L5 to pupa	27	29.80	38	5	15	20.56	34	39	12	14.58	24	19	9	12.27	28	44	9	10.17	12	6	6	7.63	11	43
L6	9	11.2	14	18	7	10	13	4	6	6	6	4	5	5	5	2	4	5	6	8	3	3	3	1
L6 to pupa	24	30.46	38	35	9	21.42	33	36	12	14.64	23	76	10	13.08	22	26	7	10	17	49	3	7.13	10	40
L7	0	9	9	0	9	9	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L7 to pupa	22	29.94	37	16	17	19.67	23	3	14	14.75	15	4	15	15	15	1	8	9.63	11	8	7	7	7	1
L8	0	21	21	0	21	21	21	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L8 to pupa	0	11	11	0	11	11	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

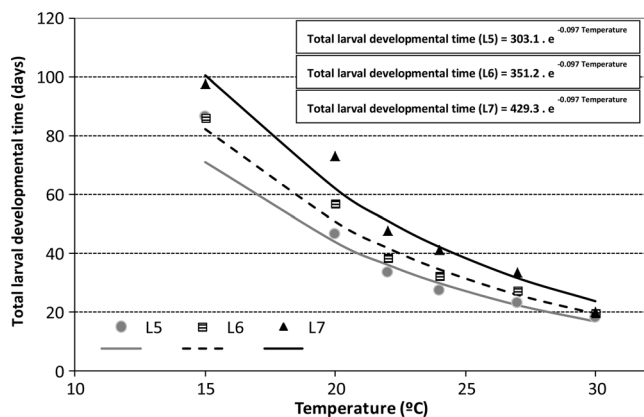


Fig 5 Mean total larval developmental time as a function of temperature, considering the last larval instar (population).

We then evaluated the mean of the total larval developmental time as a function of the temperature, considering the last larval instar before pupation (population). Although in the three populations we observed a decrease in time in the larval development to the extent that temperature increase, the adjustment was not linear, instead, we found that the exponential model was the best adjustment in all populations (Fig 5; Table 5). The correspondent equation of this model was:

$$\text{Total larval length} = k \times e^{\beta \text{ Temperature}}$$

where k is the scale parameter, e is exponential, and β is the shape parameter.

The gradient (β) was the same in the three populations, while the origin ordinate (α) increased to the extent that more larval instars existed before the pupa.

Discussion

When we recorded the developmental time of each larval instar, we found that, at all temperatures, there were mainly two groups of data after L5, which made us think of two statistical populations (L5 and L6), given that the individuals

Table 5 Estimation (\pm SE) of the parameters of the transformed equations since ANCOVA results.

Last larval instar (population)	Parameters	Estimation	SE
L5	α	5.71	0.0318
	β	-0.097	0.0012
L6	α	5.86	0.0299
	β	-0.097	0.0012
L7	α	6.06	0.0324
	β	-0.097	0.0012

could present mainly two types of behaviors or strategies after the last larval instar before pupating. This stage was not determined by temperature because there was not a clear pattern between temperature and strategy; therefore, other factor/s could be involved. This was further supported by the fact that not only 100 individuals were studied per temperature but also that the replicate conducted at 30°C showed differences with the first experiment and the other temperatures. In several species with intraspecific variability in the number of instars, some of this variation may occur in standardized rearing conditions. This could indicate that once the variability has evolved, the number of instars remains highly plastic at an intraspecific level. Some of the factors influencing this occurrence could be genetics, acquired via maternal way, and at the same time may be dependent on environmental conditions experimented by a parent (Esperk *et al* 2007). These results could be related to an adaptation when facing the environment. Furthermore, the number of larval instars may be genetically different in larvae from different populations (Nagasawa 1988, Telfer & Hassall 1999, Mira & Raubenheimer 2002), amongst genetically determined phenotypes (Hodson & Chapco 1986), or amongst descendants of different individuals from a same population (Jones *et al* 1981, Morita & Tojo 1985). This may also explain the differences found in the proportions corresponding to the last larval instar before pupating.

We thought that the developmental time of the last larval instar before pupating could be different between statistical populations, being shorter in those with a shorter developmental time, but there were no differences between them. It seems that the total developmental time could depend on the number of instars, because we found at all the temperatures that at a greater number of instars, the larval developmental time was longer. In insects, there is a threshold size characteristic of each species, which a larva must reach before metamorphosis (Nijhout 1975, 1994). Thus, additional larval instars would serve as a compensatory means in adverse conditions, when a larva fails to reach that size facing a “normal” number of larvae (Nijhout 1994). The number of instars might also increase when conditions are favorable (Esperk *et al* 2007), when it could be advantageous to go through more larval instars when the growth rates are high, reaching a large size at a relative low cost (low mortality). Indeed, it has been demonstrated repeatedly that body size can be correlated positively with several components of the fitness (Honêk 1993, Blanckenhorn 2000, Rhainds & Ho 2002, Tammaru *et al* 2002). In all our experiments, the developmental time of the larval instar, which molted to pupa, was greater than that which molted to the next larval instar. This may be a strategy to avoid further prolonging the total larval development time before a future molt.

Richardson & Goff (2001) proposed that the relationship between temperature and the total

developmental time of the cycle was linear. In our work, although it was clear that larval developmental time decreased as temperature was increased, the trend found could be adjusted to an exponential model. Our results were obtained from a greater data set than that employed by Richardson & Goff (2001).

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