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PAPER

PATHOLOGY/BIOLOGY

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Effects of Different Temperatures on the Development of *Dermestes Frischii* and *Dermestes Undulatus* (Coleoptera, Dermestidae): Comparison Between Species

ABSTRACT: Dermestidae could be useful in forensic investigations to assess the PMI as adults and larvae colonize dried remains. We reared two species of Dermestidae (*Dermestes frischii* and *Dermestes undulatus*) to understand the effects of different temperatures on the length of their whole life cycle and on their immature stages. Both species were reared at 23°C ± 0.5, RH 75% and at 26°C ± 0.5, 75% RH. Our result shows that the temperature is the main factor that influences the development of those species; in fact, increasing temperature leads to a shorter development cycle (59.8 ± 0.5 and 38.1 ± 0.2 for *D. frischii*; 50.6 ± 0.6 and 36.2 ± 0.2 for *D. undulatus*). Furthermore, we found that the number of the molts before the pupa decreases from 5–7 to 5–6 for *D. frischii* and from 4–6 to 4–5 for *D. undulatus*, respectively, at 23°C and 26°C.

KEYWORDS: forensic science, forensic entomology, dermestidae, *Dermestes frischii*, *Dermestes undulatus*, temperatures, development

The Dermestidae family contains about one hundred species throughout Italy, including *Dermestes frischii* Kugelann, 1792 and *Dermestes undulatus* Brahm, 1790.

These species are widely distributed all over the world; in fact, the presence of *D. frischii* is verified in Europe, Asia, Africa, Madagascar, and North America (1), while that of *D. undulatus* in the entire Holartic region (2).

Both species, adults and immature stages, are described to be pest of foods warehouses (3); for example, Mathai (1) described *D. frischii* to be a pest for dried fish, silkworm cocoons, and other stored products, and Khan & Naghat (4) recorded *D. undulatus* infest silkworm farms and storehouses.

For this reason, many authors studied the effects of environmental variables (mainly temperature and humidity) on the development of different species belonging to this family to prevent and counteract the economic damage they are able to produce (5–9).

Moreover, some species of Dermestidae could be useful in forensic investigations as an aid to assess the PMI. Like reported by Voigt (10), Dermestidae could be responsible for the transformation of the soft part of the body and can linger on the remains as the only colonizer of a skeletonized body; according to Schroeder (11), larder beetles (adults and larvae) are able to skeletonize a human corpse in less than five months in indoor environments, and Charabidze (12), reviewing 81 forensic case, observed a peculiar decomposition pattern with the face, hands, and feet as preferential feeding area for the Dermestidae that can completely disarticulate those areas from the body. He also describes *D. frischii* and *D. undulatus* as predominant species in outdoor cases and that if more of two species are involved in the decomposition, the association of *D. frischii* and *D. undulatus* is the most common.

However, in the case of forensic assessment it is essential to assign a certain age to the samples to trace the time of their colonization. Dating Dermestidae's immature stages is very difficult as those insects pass through a number of larval stages which vary with the species and the temperature (13); moreover, the different instars do not show typical morphological markers that could make them distinguishable.

For this reasons, it is important to understand the effects of environmental variables (temperature in the first place) on each immature stage of the life cycle of larder beetles; the only data related to this issue regard a study performed on *D. frischii* reared at a constant temperature of 27°C (8,14).

The present study was carried out to increase the knowledge related to two species (*D. frischii* and *D. undulatus*) reared at different temperatures, especially of the larval stages never tested before by other authors. In particular, the study aimed to understand the effects of different temperatures on the length of their whole life cycle and on their immature stages.

We also want to appraise whether different growth conditions could change the number of the larval stages in *D. frischii* and *D. undulatus* as happens for other species of Dermestidae (15–17).

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Material and Methods

Rearing

Adults of both species, collected in the field, were placed in different tanks thermostated at 28°C, temperature ideal for laying eggs according to Peacock (3), and were regularly provided with dried pig hides as a food substrate and moist cotton for water.

Every day the laid eggs were transferred into different jars, each one adequately supplied with food and moist cotton. These were placed inside an incubator where we set a rearing temperature of 23°C ± 0.5, RH 75% for the first trial and a temperature of 26°C ± 0.5, 75% RH for the second one. The samples were monitored every day, and particular attention was paid to the number of *exuviae* produced by the molts that witness the passage from a larval stage to the next. All the data regarding the number of the eggs and the last of the single immature stages were record and tabulated. The experiment was replicated 158 times: 39 and 48 for *D. frischii*, 49 and 22 for *D. undulatus* at 23°C and 26°C, respectively.

Statistical Analyses

We adopted the following nomenclature for statistical aims: egg (E), active larval stage (LS), prepupa larval stage (LsP), and pupa (P); developmental cycle (DC) was used to refer to the whole developmental cycle from E to P. Different larval instars within LS were numbered in sequence (e.g., LS_1 refers to the first larval stage after eggs hatching, LS_2 to the second larval stage after the first molt, etc.) starting from E to LsP, and the number of larval instars within a DC was indicated as subscript (e.g., DC_5 refers to a cycle with the LS including five larval instars).

A χ^2 test was used to check whether the frequency of jars with DC differing for the number of larval instars changed between temperature treatments within species. Two samples *t*-test were used to check whether mean durations of larval instars differed between species or treatments. Then, a one-way analysis of variance (ANOVA) was used to check for significant differences in the duration of larval instars within LS, and a separate analysis was performed for each DC in each temperature and species.

Finally, to check whether the duration of E, LS, LsP, and P differed between temperature treatments and species, we fitted a generalized linear mixed model on a Bayesian mode of inference. The model design included stage duration as dependent variable, whereas the species, the temperature treatment, the larval developmental stages, and all possible interactions were the fixed effects. The jar was included as random effect. As no a *priori* information was available, a non-informative Gaussian prior ($m = 0$ and $\sigma=10^{10}$) was used for the fixed effects, and a non-informative inverse Wishart prior ($V = 1$ and $\eta=0.002$) was used for all variances. Markov chain Monte Carlo (MCMC) methods were used to obtain an arbitrarily large sample of draws from the posterior distributions for inference. Chains were allowed to run for 10^6 iterations with a burn-in of 10,000 iterations and a thinning interval of 100, obtaining 9900 draws of the posterior distributions for inference. This led to a good convergence as evaluated by the diagnostics plots. Credible intervals (CI) including zero were regarded as nonsignificant. To check for significant effects of the interactions, we used the deviance information criterion (DIC) to compare the Bayesian MCMCglmms including and not including the interaction of interests. DIC is a parameter estimating the performance of a Bayesian model on the basis of deviance and of the effective number of parameters. Models having lower deviance and less effective parameters show lower DIC and are considered the models most appropriate to the dataset (18).

Statistical analyses were performed using R ver.3.1.0 (RCoreTeam2014, Vienna, Australia), whereas the Bayesian models were performed using the MCMCglmm package (19). Otherwise stated, reported values represent means and standard errors.

TABLE 2—*Mean (±SE) duration (days) of the egg stage (E), active larval stage (LS), prepupa larval stage (LsP), pupa (P), and developmental cycle (DC) of* Dermestes frischii *and* Dermestes undulatus.

	E	LS	LsP	P	DC
Dermestes frischii					
T = 23°C	3.9 ± 0.1	25.8 ± 0.7	18.9 ± 0.7	11.2 ± 0.1	59.8 ± 0.5
T = 26°C	2.9 ± 0.1	13.6 ± 0.3	13.4 ± 0.3	8.2 ± 0.1	38.1 ± 0.2
Dermestes undulatus					
T = 23°C	4.4 ± 0.3	17.1 ± 0.8	17.5 ± 0.5	11.6 ± 0.2	50.6 ± 0.6
T = 26°C	3 ± 0	10.5 ± 0.6	14.1 ± 0.4	8.7 ± 0.2	36.2 ± 0.2

Results

Both species exhibited typical behavior for Dermestidae; like described by Peacock (3), the females laid their eggs in small groups in the folds of the food substrate and the maggots remain

TABLE 1—*Comparison (one-way ANOVA) among mean (±SE) duration (days) of each larval instar of* Dermestes frischii *and* Dermestes undulatus *according to the different DCs; within each row means having the same letters in different from each other at 0.05 significance level.*

		N	LS_1	LS_2	LS_3	LS_4	LS_5	LS_6	F	d.f.	*p*
Dermestes frischii											
T = 23°C	DC_4	1	4	5	9	3	–	–			
	DC_5	24	$5.2^{a} \pm 0.3$	$4.6^{b} \pm 0.2$	$4.1^{b} \pm 0.2$	$4.2^{b} \pm 0.2$	$5.3^{a} \pm 0.3$	–	6.545	4,115	<0.001
	DC_6	14	$6.3^{a} \pm 0.7$	$5.1^{b} \pm 0.4$	$4.5^{b} \pm 0.2$	$4.3^{b} \pm 0.2$	$4.2^{b} \pm 0.3$	$5.5^{ab} \pm 0.3$	4.455	5,78	0.001
T = 26°C	DC_4	26	$3.0^{a} \pm 0.1$	$3.2^{a} \pm 0.1$	$2.7^{b} \pm 0.1$	$2.9^{ab} \pm 0.1$	–	–	3.675	3,100	0.015
	DC_5	22	$3.9^{a} \pm 0.2$	$3.1^{b} \pm 0.1$	$3.1^{b} \pm 0.1$	$2.8^{b} \pm 0.1$	$3.0^{b} \pm 0.1$	–	10.643	4,105	<0.001
	DC_6	0	–	–	–	–	–	–			
Dermestes undulatus											
T = 23°C	DC_3	26	$5.3^{a} \pm 0.3$	$3.8^{b} \pm 0.3$	$4.6^{a} \pm 0.2$	–	–	–	8.474	2,75	<0.001
	DC_4	20	$5.4^{a} \pm 0.4$	$5.3^{a} \pm 0.3$	$4.2^{a} \pm 0.4$	$4.7^{a} \pm 0.3$	–	–	2.293	3,76	0.085
	DC_5	3	$4.2^{a} \pm 0.7$	$6.9^{b} \pm 0.9$	$5.3^{ab} \pm 0.5$	$3.6^{a} \pm 0.3$	$4.5^{a} \pm 0.5$	–	4.044	4,10	0.033
T = 26°C	DC_3	15	$3.4^{a} \pm 0.1$	$2.8^{b} \pm 0.1$	$2.8^{b} \pm 0.2$	–	–	–	6.117	2,42	0.005
	DC_4	7	$4.6^{a} \pm 0.8$	$3.3^{b} \pm 0.1$	$3.1^{b} \pm 0.2$	$2.5^{b} \pm 0.2$	–	–	4.682	3,24	0.010
	DC_5	0	–	–	–	–	–	–			

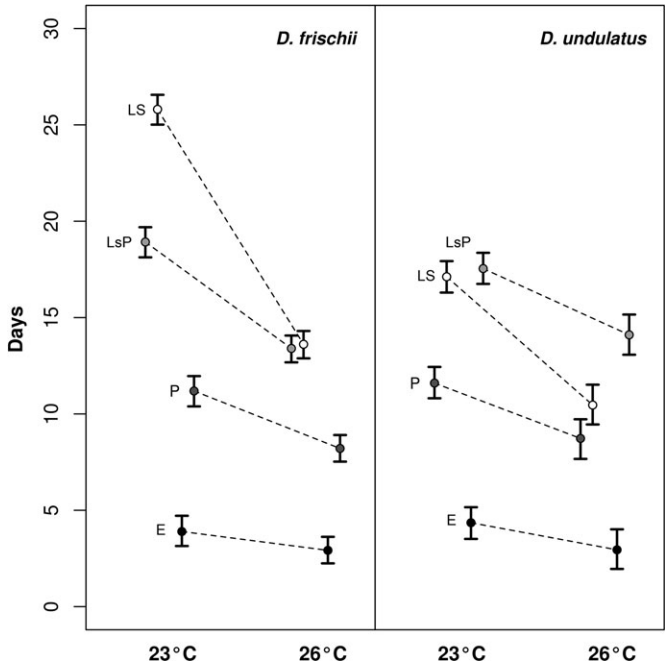

FIG. 1—*Mean Durations of the egg stage (E), active larval stage (LS), prepupa larval stage (LsP), and pupa (P) of* Dermestes frischii *and* Dermestes undulatus *incubated at 23°C and 26°C respectively. Bars represent 95% confidence intervals for the means.*

on the same substrate until the last instar (LsP) when they stop eating and sought shelter near the moist cotton to pupate.

The larvae vary in color from dark brown to black except in the moments following the hatching of eggs and the molts. Adults appeared whitish in the hours following the emergence and reached the characteristic color of the species within 24 h.

Number and Duration of Larval Stages (LS)

Of the 39 jars obtained at 23°C for *D. frischii*, one DC_4 (2.6%), 24 DC_5 (61.5%) and 14 DC_6 (35.9%) were observed. When the jars were incubated at 26°C, these proportions significantly changed (χ^2=36.20, d.f. = 2, $p < 0.001$), and the proportion of DC_4 and DC_5 shifted to 26 (54.2%) and 22 (45.8%), respectively, while no DC_6 was obtained.

Irrespective of temperature, most cycles observed for *D. undulatus* jars were DC_3 or DC_4 (68 of 71), and only 3 were DC_5. The proportion of DCs differing for the number of larval instars did not significantly change between temperature treatments (χ^2=0.428, d.f. = 1, $p = 0.51$, DC_5 was excluded from the test), the DC_3 or DC_4 being 26 (53.1%) and 20 (40.8%) at 23°C and 15 (68.2%) and 7 (31.8%) at 26°C.

The mean durations of LS were similar between species; at 23°C, LS lasted 4.8 ± 0.1 days for *D. frischii* and 4.7 ± 0.1 days for *D. undulatus* (two-sample *t*-test: $t_{77.2}$=0.480, $p = 0.63$), while at 26°C, it lasted 3.0 ± 0.1 days for *D. frischii* and 3.1 ± 0.1 days for *D. undulatus* (two-sample *t*-test: $t_{29.8}$=0.825, $p = 0.42$). By contrast, in both species the mean duration of LS significantly decreased with increasing temperature (two-sample *t*-test, *D. frischii*: $t_{58.3}$= 19.051, $p < 0.001$; *D. undulatus*: $t_{68.6}$= 9.768, $p < 0.001$). However, significant differences among instars' duration were found within LS for each species at each temperature treatment (Table 1 for one-way ANOVA's statistics). In general, the LS_1 was significantly longer than LS_2, while the middle instars appeared to be significantly shorter than the first and last ones.

Effects of Temperature on the Larval Developmental Cycle

Thirteen jars for *D. frischii* and one for *D. undulatus* were excluded from the analyses on larval stages' duration as neither

TABLE 3—*Contrasts among developmental stages for each temperature treatment in each species estimated using a Bayesian generalized linear model.*

		E	LS	LsP
Dermestes frischii				
LS	T = 23°C	21.91 (20.87–23.07) $p < 0.001$		
	T = 26°C	10.69 (9.70–11.64) $p < 0.001$		
LsP	T = 23°C	15.02 (13.95–16.17) $p < 0.001$	−6.90 (−7.99 to −5.78) $p < 0.001$	
	T = 26°C	10.47 (9.44–11.40) $p < 0.001$	−0.21 (−1.19–0.77) $p = 0.67$	
P	T = 23°C	7.30 (6.15–8.39) $p < 0.001$	−14.61 (−15.77 to −13.52) $p < 0.001$	−7.73 (−8.82 to −6.62) $p < 0.001$
	T = 26°C	5.30 (4.32–6.26) $p < 0.001$	−5.40 (−6.33 to −4.38) $p < 0.001$	−5.18 (−6.15 to −4.17) $p < 0.001$
Dermestes undulatus				
LS	T = 23°C	12.77 (11.62–13.90) $p < 0.001$		
	T = 26°C	7.51 (6.07–8.95) $p < 0.001$		
LsP	T = 23°C	13.20 (12.07–14.37) $p < 0.001$	0.42 (−0.75–1.53) $p = 0.46$	
	T = 26°C	11.15 (9.70–12.56) $p < 0.001$	3.64 (2.24–5.13) $p < 0.001$	
P	T = 23°C	7.24 (6.14–8.39) $p < 0.001$	−5.52 (−6.68 to −4.37) $p < 0.001$	−13.19 (−14.30 to −12.04) $p < 0.001$
	T = 26°C	5.78 (4.28–7.19) $p < 0.001$	−1.73 (−3.22 to −0.32) $p = 0.020$	−5.38 (−6.85 to −3.92) $p < 0.001$

Data represent posterior means and 95% credible intervals.

TABLE 4—*Contrast between species (*Dermestes undulatus *vs.* Dermestes frischii*) for the duration of each developmental stage within each temperature treatments estimated using a Bayesian generalized linear model.*

	E	LS	LsP	P
T = 23°C	−0.45 (−0.67–1.54) $p = 0.43$	−8.69 (−9.80 to −7.57) $p = 0.0001$	−1.38 (−2.56 to −0.29)$p = 0.015$	−0.41 (−0.70–1.55) $p = 0.48$
T = 26°C	−0.04 (−1.20–1.32) $p = 0.95$	−3.16 (−4.35 to −1.87) $p = 0.0001$	−0.72 (−0.53–1.96)$p = 0.26$	−0.52 (−0.72–1.80) $p = 0.42$

Data represent posterior means and 95% credible intervals.

TABLE 5—*Variation of the developmental stage duration with increasing temperature for* Dermestes frischii *and* Dermestes undulatus *estimated using a Bayesian generalized linear model.*

	E	LS	LsP	P
Dermestes frischii	−0.98 (−2.05–0.04) $p = 0.067$	−12.19 (−13.21 to −11.09) $p = 0.0001$	−5.52 (−6.57 to −4.48) $p = 0.0001$	−2.97 (−4.06 to −1.97) $p = 0.0001$
Dermestes undulatus	−1.40 (−2.71 to −0.08) $p = 0.040$	−6.66 (−7.99 to −5.35) $p = 0.0001$	−3.44 (−4.72 to −2.08) $p = 0.0001$	−2.87 (−4.16 to −1.52) $p = 0.0001$

Data represent posterior means and 95% credible intervals.

of the individuals developed into a pupa. Consequently, the sample included 74 jars (of which 38 at 23°C and 36 at 26°C) for *D. frischii* and 70 jars (of which 48 at 23°C and 22 at 26°C) for *D. undulatus*. Mean durations of developmental stages for each species in each temperature are reported in Table 2. The mean duration of the whole cycle was significantly longer in *D. frischii* than in *D. undulatus* either at 23°C (*D. frischii*: 59.8 ± 0.5 days; *D. undulatus*: 50.6 ± 0.6 days; two-sample *t*-test: t_{72}= 5.781, $p < 0.001$) or at 26°C (*D. frischii*: 38.1 ± 0.2 days; *D. undulatus*: 36.2 ± 0.2 days; two-sample *t*-test: t_{68} = 0.59 9, $p < 0.001$). Furthermore, in both species the mean duration of the whole cycle significantly decreased with increasing temperature (two-sample *t*-test, *D. frischii*: t_{17}=5.084, $p < 0.001$; *D. undulatus*: t_{17}=4.092, $p < 0.001$).

The MCMCglmm including the three-way temperature × species × larval developmental stages obtained the lowest DIC (the difference in DIC between models exceeded 24), suggesting that the extent of the differences in duration among larval developmental stages changes between temperature treatments, and those patterns also varied between species (Fig. 1). In detail, the stages E and P were the faster in both species and temperature treatments, E being always significantly faster than P (Table 3, Fig. 1). In *D. frischii,* the LS stage was significantly longer than the LsP one, but only at 23°C, because at 26°C, the two stages did not differ significantly; the opposite occurred in *D. undulatus*; LS stage was shorter than LsP at 26°C, but the two stages were similar at 23°C (Table 3, Fig. 1). The stages E and P did not differ between species in both temperature treatments, whereas *D. frischii* with respect to *D. undulatus* showed significantly longer LS and LsP, the last one only at 23°C (Table 4, Fig. 1). Finally, the duration of all immature developmental stages significantly decreased from 23°C to 26°C, with the exception of the E stage of *D. frischii* only (Table 5, Fig. 1). Furthermore, the change in LS was more pronounced in *D. frischii* than in *D. undulatus* (Table 1).

Conclusions

The effects of different growing temperatures on the development of *D. frischii* was examined by several authors, although they evaluated only the entire cycle without considering how the temperatures affect each immature stage.

Andres (5) reared the species at 28–30°C and obtained a complete development of the larvae in 22–25 days; subsequently, Howe (6) evaluated the effects of different temperature, with a relative humidity ranging between 40% and 70%: He found that the minimum cycle was of 29–31 days at 33°C and the maximum was of 111–115 days at 20°C. In addition, he identified as optimum temperature growth range the one between 30°C and 33°C (7). Amos (8) in contrast determined a minimum period of development for this species of 26–27 days at 35°C with a relative humidity of 90%.

Furthermore, Howe (6) identified 40°C as limiting temperature for the development of *D. frischii* as all the specimens that he examined died during the larval stage.

In relation to the temperature tested in this study, our results agree with those of the quoted authors. In fact, the length of the development cycle decreases with the increasing temperatures; in addition, we have shown that the temperature has a statistically significant effect on the growth of *D. frischii*.

In particular, by analyzing the development cycle in each instar, it has been shown how the effects of different temperatures are mainly expressed on the larval stages, not on their average length but, rather, on their number. This is similar to the response of other Dermestidae such as *Dermestes maculatus* that have from 5 to 11 larval instar depending on the environmental conditions of development (15,16) or *Dermestes lardarius* that developed 5–10 instar according to different growing conditions (17).

We have observed that the length of the entire development cycle (DC) of *D. frischii* declines with increasing temperature from 23°C to 26°C due to the loss of an active larval stage (LSn) before pupa.

This is evident considering the variation, in the percentage, of cases in which *D. frischii* exhibits development cycles DC_4, DC_5, or DC_6 that passes, respectively, from 2.6%, 61.5%, and 35.9% rearing the species at 23°C to 54.2%, 54.2%, and 0 at 2°C.

For this species, we found that the number of the molts before the pupa decreases from 5–7 at 23°C to 5–6 at 26°C.

With respect to *D. undulatus*, Zhantiev (9) reared this species at 22°C (RH 50–60%) noting that its life cycle, from egg to adult, varied between 62 and 76 days, the incubation period lasting 5–6 days, the larval period 40–60, and the pupa 11 days.

Also, he showed that an increasing temperature causes a shorter duration of the whole development cycle. But our results show that the proportion between development cycles with different LSn (in this case DC_3 and DC_4) does not change significantly between 23°C and 26°C. However, in the first case the species developed 4–6 molts before the pupa, while only 4–5 in the second one, and at 26°C, LS is significantly shorter compared to only LsP, while at 23°C, they have comparable duration. These results lead us to conclude that also for this species, the temperature has the same effect it has on the development of *D. frischii*.

In both species, rise of the temperature causes a significant decrease in the entire immature development cycle. However, it is important to note that at 23°C and at 26°C, *D. frischii* always exhibits a significantly longer development period than *D. undulatus* demonstrating that there is a distinct difference between the two species despite the fact that they respond similarly to the environmental changes.

Regardless of the species, the effect of temperatures on LS rather than on E, LsP or P may be linked to the extreme sensitivity of this phase to growth conditions as suggested by Bellemare & Brunelle (15). They identify the larval stages as the most critical, less stable and thus more variable among the immature stages. Our hypothesis is that these insects react to the unfavorable development conditions extending LS to accumulate more nutrients useful during the LsP and P stages in preparation to the metamorphosis that will lead to adults. According to Esperk (20), additional larval instar to the "normal" number could be a mechanism to react at adverse environmental conditions, so the insect could develop more instar to achieve a certain threshold before pupation; in particular, many species perceive low temperatures as a cue for unfavorable season that conduce to the development of a higher instar number.

He also reports that other factors such as humidity, photoperiod, sex dimorphism, food quantity and quality, injuries, and inheritance could affect the number of instars (20).

However, in forensic case it is impossible to evaluate the effect of those factors (except for humidity and photoperiod) on the development of the specimens found on a cadaver. Instead, it is important to understand the effects of environmental variables.

In particular, for Dermestidae evaluating the development time of the specimens found on a corpse in relation to the environmental conditions of the site of the discovery could lead the entomologist to assess the beginning of the dehydration of the remains as both adult and larvae carry on them the entire development cycle.

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