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Keywords *Dermestes*; Coleoptera; decay; thermogenesis; forensic entomology.

ABSTRACT

This article discusses the ability of adults of the coleopteran beetle *Dermestes maculatus* (De Geer) to colonise fresh remains. It also considers whether colonisation results in localised thermogenesis in a similar manner to that induced by blowfly larvae.

In the laboratory, adult *D. maculatus* instantly colonised fresh killed rats and mice. The adults entered the oral cavity within 1-2 hours and the eyes and ears were among the first parts of the body consumed. Egg laying occurred on the torso and head within an hour of death and eggs hatched within 3-4 days. The larvae remained on the body whilst the adults (>70%) rested in the surrounding wood chippings when not feeding or laying eggs. Larvae grew rapidly on the dead bodies and some were starting to pupate within 28 days.

The dermestids consumed the corpses predominantly from the head downwards and weight loss correlated with the number of larvae produced. In both rats and mice, colonisation of the abdominal region was associated with an increase in temperature. The maximum abdominal temperature and the length of time the temperature remained 1^{o}C or more above ambient correlated with the number of larvae produced. This rise in temperature would probably be sufficient to increase the rate of development of dermestid larvae and that of any other invertebrate or microbe in the region. In the absence of dermestids, the internal temperature rarely rose 1^{o}C above ambient.

Although there are previously published accounts of dermestid beetles consuming fresh corpses, they are reputed to favour older desiccated remains. This paper confirms that *D. maculatus* rapidly consumes and reproduces on fresh remains. The fact that dermestid beetles are seldom found on fresh remains under field conditions is therefore probably a result of inter-specific competition among decomposing insects

rather than food preference. This information could be useful when determining the forensic significance of *D. maculatus* recovered from dead bodies.

Keywords
Dermestes; Coleoptera; decay; thermogenesis; forensic entomology.

1. Introduction

The family Dermestidae currently contains over 1000 species and includes many common household and stored product pests [1,2] but most of the dermestid beetles recovered from dead humans belong to just a few species of the genus *Dermestes* [3,4]. Members of the genus *Dermestes* are often referred to as skin beetles whilst their larvae are known as 'wooly bears' as a consequence of their numerous long setae. In France, it was found that in 81 cases in which dermestid beetles were recovered from dead bodies, *Dermestes frischii* (Kugelmann) and *Dermestes undulatus* (Brahm) accounted for the majority of infestations (42% and 35.8% respectively) [3]. Similarly, in Turkey, *D. frischii* and *D. undulatus* are the most common dermestid beetles on pig carcasses [5].

Dermestes maculatus (De Geer) is a cosmopolitan species that occurs in Europe, North and South America as well as Asia. In common with many dermestid beetle species, it requires a warm climate to complete its development. It takes an average of 27 days to reach adulthood at 30^{o}C and 74 days at 20^{o}C [6]. Consequently, it occurs usually within buildings and human dwellings in the UK and Northern Europe. It is well known as a pest of stored dry animal products and is common in both domestic and commercial settings. The frass and larval setae may cause allergic reactions [7]. *D. maculatus* are sometimes recovered from human remains and have occasionally been used as indicators of the post-mortem interval [8]. In countries with cool temperate climates *D. maculatus* are usually associated with bodies found indoors. For example, in Germany Schroeder et al. [9] describe a case in which the body of an adult man was skeletonised by dermestids within 5 months of him dying in his apartment. They assumed that this was subsequent to his body mummifying although as will be discussed later, colonisation may actually have begun a lot earlier. By contrast, in countries with hot climates such as South Africa and Brazil *D.*

maculatus is also likely to colonise bodies exposed outside in the natural environment [10, 11].

Whilst not as commonly recorded on bodies as blowflies, dermestid beetles were found in 7.5% of 1,093 cases investigated by French forensic entomology laboratories [3]. Drug residues are detectable in dermestids that have fed on remains containing them and therefore they may have potential in entomotoxicology [12]. Unfortunately, larval dermestids cannot provide the same level of accuracy for the determination of the minimum time since death as can the larvae of blowflies. This is because the larvae lack morphological indicators of instar number and, at least in some dermestids (e.g. *Trogoderma glabrum* Herbst), a reduction in food supply can result in 'regressive moults' in which the larvae become progressively smaller [13] whilst in others, such as *Dermestes lardarius* (L.), adverse conditions can result in extra instars and prolonged development times [14]. Consequently, it is impossible to determine a larva's instar or age from its size.

The aims of the present study were to assess whether *D. maculatus* would colonise fresh remains and whether their feeding induced localised thermogenesis.

2. Methods

2.1. Beetles and Rearing Conditions

Culture conditions: The colonies of *D. maculatus* used in these experiments had been in laboratory culture for 48 months. The insects were maintained in clear plastic tanks (30cm length x 19cm width x 19cm height) in an indoor insectary maintained at 23 $\pm$ 1^{o}C and a 12h:12h light: dark regime. There was a 2cm layer of wood chippings at the base of the tanks and polystyrene packaging provided a medium into which the mature larvae could burrow when they were ready to pupate.

2.2. Colonisation of freshly dead rats and mice

Adult male rats (399.16-521.97g) and female mice (19.56-24.06g) were humanely euthanized using carbon dioxide and then weighed. There was no significant difference in the average weights of rats (ANOVA, $F_{2,11} = 0.756$, $P = 0.493$) and mice (ANOVA, $F_{1,10} = 0.091$, $P = 0.769$) used in the different treatment groups.

Each rat had a lead from a HOBO® U23-003 PRO V2 temperature data logger inserted via the rectum into the hindgut to record abdominal temperature. Owing to their smaller size, the abdominal temperatures of the mice were recorded using Elitech® RCA-4 Mini Temperature Data Loggers. The loggers recorded the temperature every 10 minutes. Separate data loggers recorded the ambient air temperature in the insectary.

The experiments took place within clear plastic tanks kept in the same insectary as the culture colonies. The dead rats were placed in 30cm length x 19cm width x 19cm height tanks whilst the mice were placed in tanks measuring 20cm length x19cm height x 19cm width. Both types of tank had a 2cm layer of wood chippings at the base and a cloth placed over the top to prevent escapes and other insects accessing the dead animals.

Adult, mixed sex, *D. maculatus* were added to the tanks 15 minutes before the dead animals were introduced. Either 50 (3 replicates) or 100 (6 replicates) adult beetles were added to the rat tanks and 20 (4 replicates) to each of the mouse tanks. Controls consisted of dead rats (5 replicates) and mice (8 replicates) without dermestid beetles set up in an identical manner at the same time as the experimental tanks.

The tanks were re-weighed after 6 hours and then every 24 hours for either 28 days (rats) or 24 days (mice). At the time of weighing, observations were made on the state of decay and the activities of the insects. The mice were observed for a shorter duration because by day 24 the dermestids had completely skeletonised their corpses. At the end of the observations, the numbers of insects in each tank were counted.

2.3. Statistical analysis

Descriptive statistics, ANOVA, and Spearman's Rank correlation analyses were performed using SPSS (version 24). Because the rats and mice were observed for different lengths of time, direct statistical comparisons between them are not appropriate.

3. Results

3.1. Colonisation of freshly-dead rats and mice

Adult beetles investigated the dead rats and mice almost immediately and began feeding within 5 minutes. The oral cavity and ear canals were invariably explored and the eyes were often consumed within 24-48 hours. Feeding was usually communal with several insects feeding in close proximity to one another. The foot pads and ear lobes were also attacked within the first 48 hours although it was common for just one ear lobe or foot pad to be extensively consumed whilst the other(s) were not touched until several days later. Although adult beetles fed around the anus, penis, and testicles in the rats and the anus and vagina in the mice, they consumed the bodies primarily from the head downwards. The first holes chewed into the body were always in the throat and upper thorax. The abdominal region was not exposed until after the body had deflated and the upper body was becoming skeletonised. The beetles chewed numerous slits into the skin rather than extending a single large entry point (Fig. 1a). In rats, the presence of dermestids significantly reduced the length of the bloat stage of decomposition (ANOVA $F_{2,13} = 20.14$, $P < 0.001$). In the control rats, the duration of the bloat stage was prolonged (12.2 $\pm$ 0.58 days, Tukey post hoc $P<0.001$) and their skin surface remained unbroken for the duration of the experiment. There was no difference (Tukey post hoc $P>0.05$) between the time until the onset of deflation between starting densities of 50 adult dermestids (9.3 $\pm$ 0.33 days) and100 adult dermestids (7.8 $\pm$ 0.48 days). However, there was a negative correlation between the time until the onset of deflation and the number of larvae produced (Spearman's correlation rho = -0.927, $P<0.001$, Fig. 2). Unfortunately, the time taken until deflation was not recorded for the mice. In all rats and mice, the rise in internal body pressure associated with bloat caused the expulsion of fluids from the mouth and anus.

a b

Fig. 1. (a) Post-mortem wounds in a dead rat caused by the feeding activity of *Dermestes maculatus*. Note the thin flecks of moist frass rather than long thin strands normally associated with dermestid beetles. (b) *D. maculatus* feeding and laying eggs on a rat that was dead for 24 hours and entering the bloat stage of decomposition.

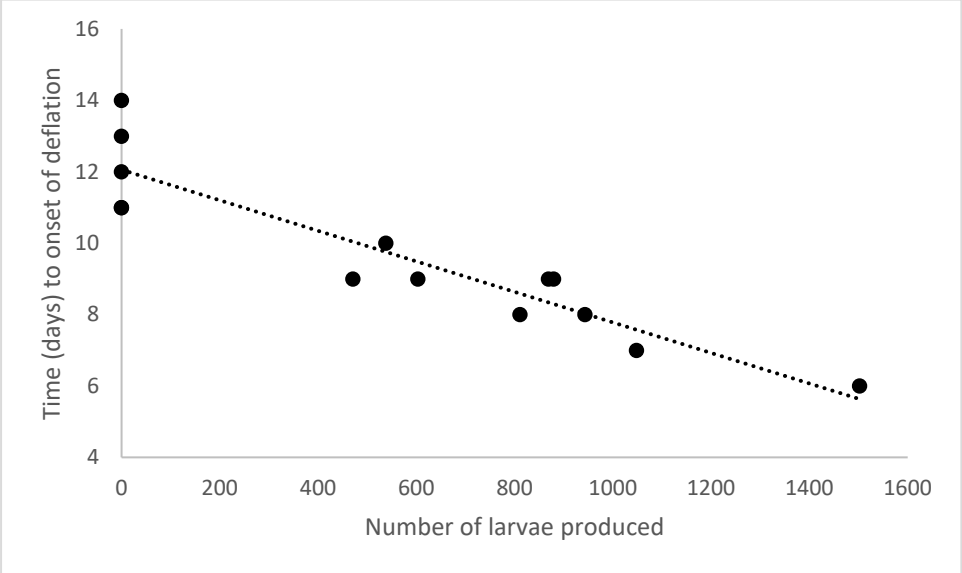


Fig. 2. The influence of the total number of *Dermestes maculatus* larvae produced on the time taken until the onset of deflation (end of the bloat stage) of dead rats. Dotted line = linear trend line.

Most of the adult beetles spent their time resting in the wood chippings and only accessed the rats and mice when feeding, mating, or laying eggs (Fig. 3). Similar proportions of beetles were observed on both the rats and mice over the first 10 days. On rats, at a starting density of 100 beetles, it was impossible to count the number of adult insects beyond day 15, whilst at a starting density of 50 beetles they could be counted up until day 17. Counting became impossible because of a combination of insects entering the body cavity and them being obscured by fur detaching from the body. However, in both cases there was a drop in the number of adults present on the corpses in the preceding days. On mice, it was not possible to count accurately the adult beetles on the bodies after day 16.

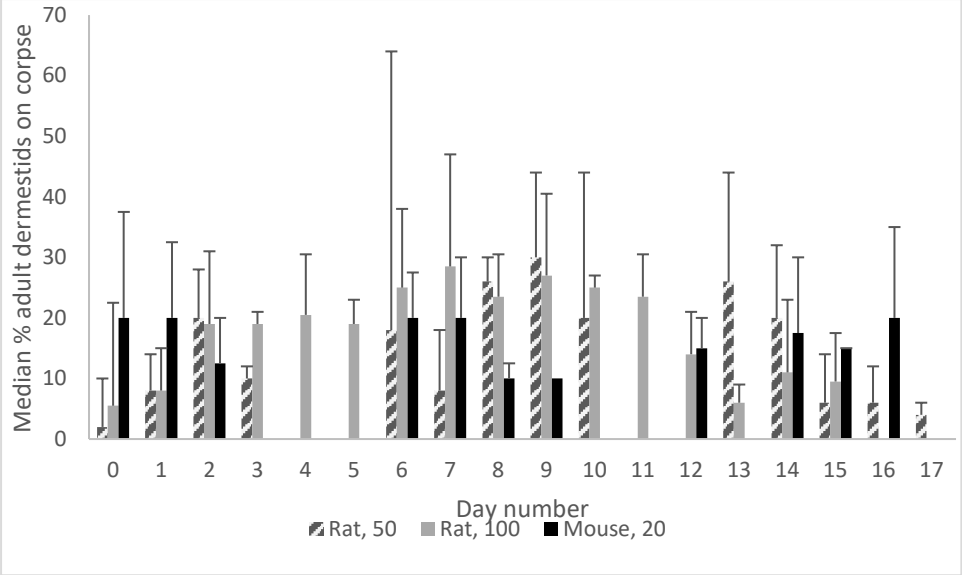
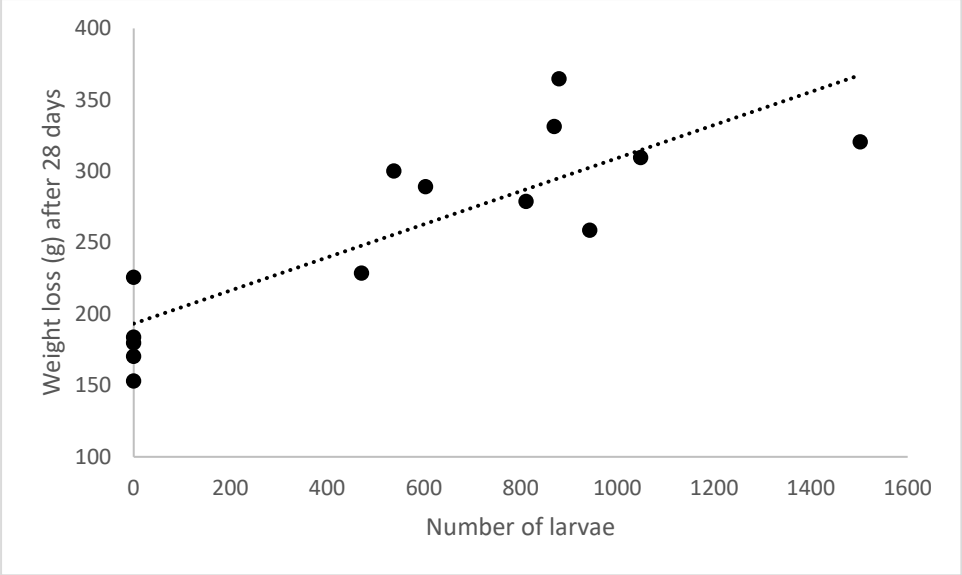


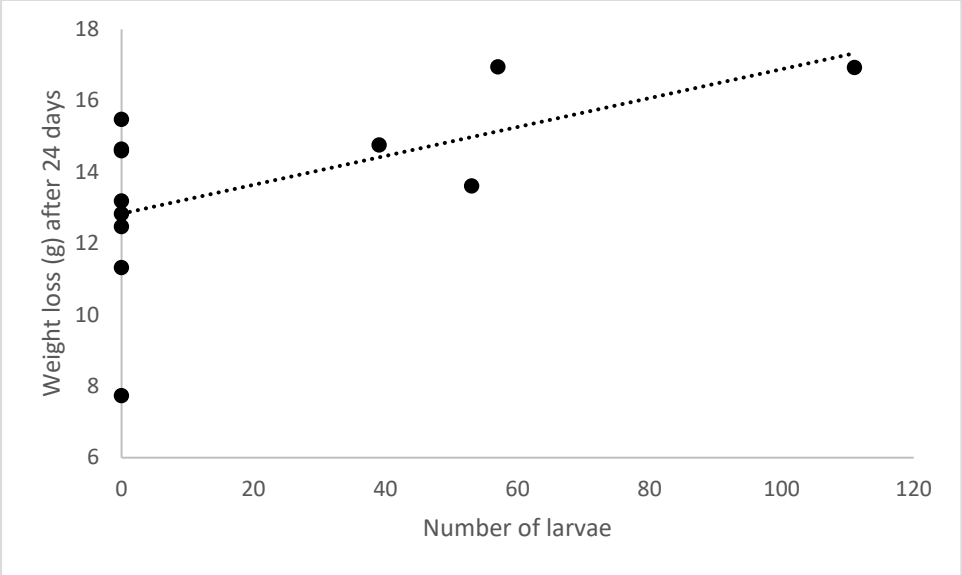
Fig. 3.The median percentage + interquartile range of adult *Dermestes maculatus* observed on rat and mouse corpses during the initial decay period under laboratory conditions. Rats had a starting density of either 50 or 100 adult beetles. The mice had a starting density of 20 adult beetles. Day 0 = 6 hours after introducing the corpses to the beetles. Recording ceased when the corpses were too decomposed to count the beetles accurately.

3.2. Weight loss

After 28 days, the control rats lost a median of 36.1% (IQ range = 10.55) of their initial weight and were starting to dry out. The control mice dried out much more rapidly and by day 24 they had lost a median of 59.9% (IQ range = 10.55) of their body weight. By the end of the observations, the rats exposed to 100 adult dermestids and the mice exposed to 20 dermestids were almost completely skeletonised and had lost medians of 61.6% (IQ range = 4.6) and 70% (IQ range = 1.9), respectively of their initial body weight. The rats exposed to 50 adult dermestids lost a median of 55.5% (IQ range = 11) of their body weight over 28 days. On both the rats and the mice, the loss of weight correlated with the number of larvae produced: rats: Spearman's correlation rho = 0.838, P = <0.01, n = 14; mice: Spearman's correlation rho = 0.649, P = <0.05, n = 12, Fig. 4 a,b).



a



b

Fig. 4. The influence of the number of *Dermestes maculatus* larvae produced on weight loss of dead rats (a) and mice (b). Dotted line = linear trend line

3.3. Reproduction

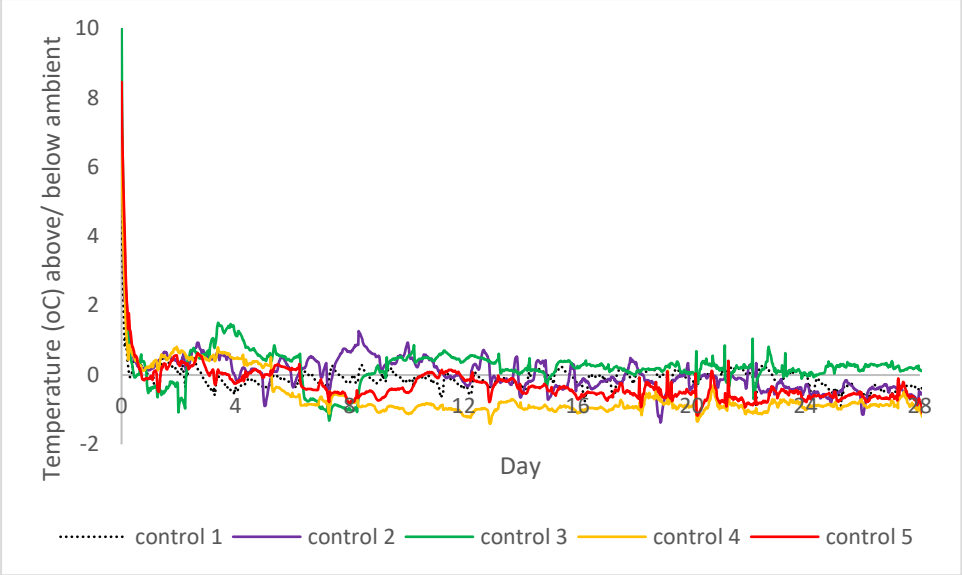
In some cases, oviposition occurred within 5 minutes of the adults gaining access to the dead animals. The female beetles inserted their ovipositor into the skin and laid their eggs immediately beneath the skin surface (Fig. 1b). Oviposition occurred on all rats and mice within 48 hours and the first larvae were seen on day 3. The larvae remained on the dead bodies and fed communally. At the end of the observation period, on both the rats and the mice, there was a mixture of larval sizes.

These included a small proportion of larvae that had recently hatched (rats: median = 1.6%, IQ range = 1.84; mice: median 9.3%, IQ range = 10.79). On all the rats, by day 28, most larvae were large (>12mm) (median = 74.0%, IQ range = 23.47) and some were starting to pupate (median = 3.3%, IQ range = 3.45). Insects that were ready to pupate moved away from the dead bodies and burrowed into the polystyrene packing provided. On the mice, on day 24, all the larvae were of medium size (8-12mm) or smaller.

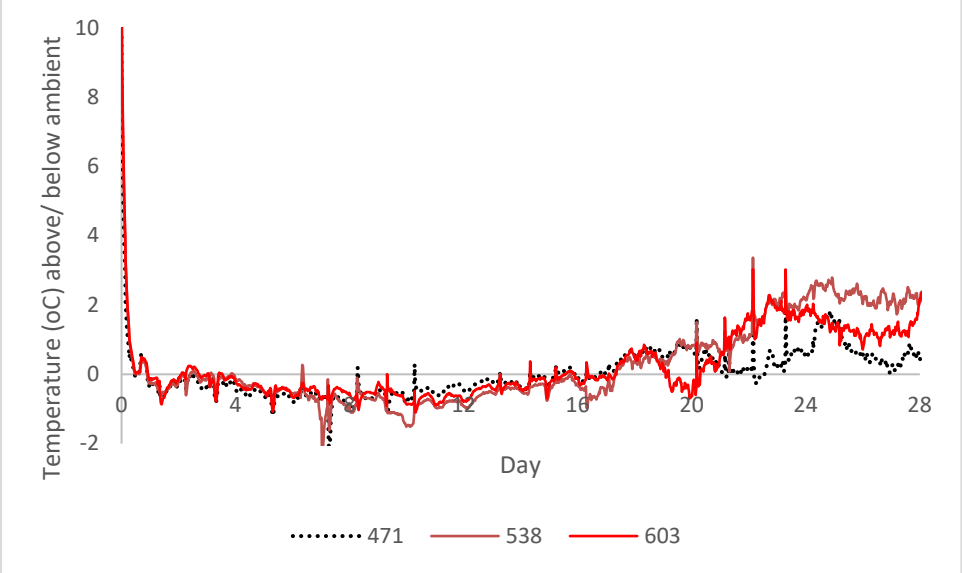
The number of larvae produced per adult by the dermestids feeding on mice was lower (average $\pm$ SE = 3.3 $\pm$ 0.79) than that produced by 50 and 100 adults per rat (average $\pm$ SE = 10.7 $\pm$ 0.76 and 10.1 $\pm$ 1.04 respectively). However, because the rats and mice were exposed to beetles for different lengths of time, direct statistical comparisons between them are not appropriate. On rats, there was no difference in the number of larvae produced per adult (T test t = 0.412, df = 7, P>0.695) by the two initial adult densities of dermestids.

3.4. Abdominal temperature

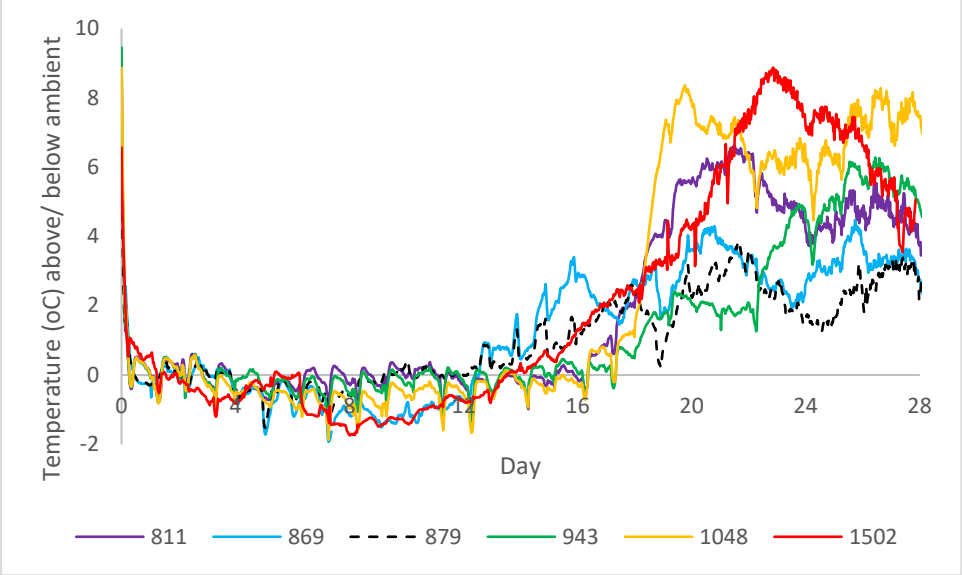
In the absence of dermestids, the abdominal temperature of dead rats (Fig. 5a) and mice (Fig. 6a) rarely rose 1^{o}C above ambient and the maximum was reached within the first few days: rats = 3.8 $\pm$ 1.17 days; mice = 2.0 $\pm$ 0.87 days. Indeed, the abdominal temperature was usually slightly below ambient. By contrast, in the presence of dermestids, in both rats (Fig. 5 b,c) and mice, (Fig. 6b) there was a rise in the abdominal temperature towards the end of the observation period. This rise coincided with the consumption of the abdominal region by the insects. In both rats and mice the maximum abdominal temperature correlated with the number of larvae produced: rats: Spearman's correlation rho = 0.942, *P* = <0.01, n = 14; mice: Spearman's correlation rho = 0.828, P = <0.01, n = 12 (Fig. 7 a,b). The duration over which the abdominal temperature remained at least 1^{o}C above ambient also correlated with the number of larvae produced: rats: Spearman's correlation rho = 0.847, *P* = <0.01, n = 14; mice: Spearman's correlation rho = 0.97, *P* = <0.01, n = 12 (Fig. 8 a, b). In rats and mice exposed to dermestids, maximum abdominal temperature was reached after 22.8 $\pm$ 0.71 days and 22.6 $\pm$ 0.70 days respectively. If the zero dermestid controls were excluded, there was no correlation between the number of larvae produced and time taken to reach maximum temperature in both rats and mice (Fig. 9 a,b).


Temperature (oC) above/ below ambient
10
8
6
4
2
0
-2
0
4
8
12
16
20
24
28
Day
control 1
control 2
control 3
control 4
control 5

a

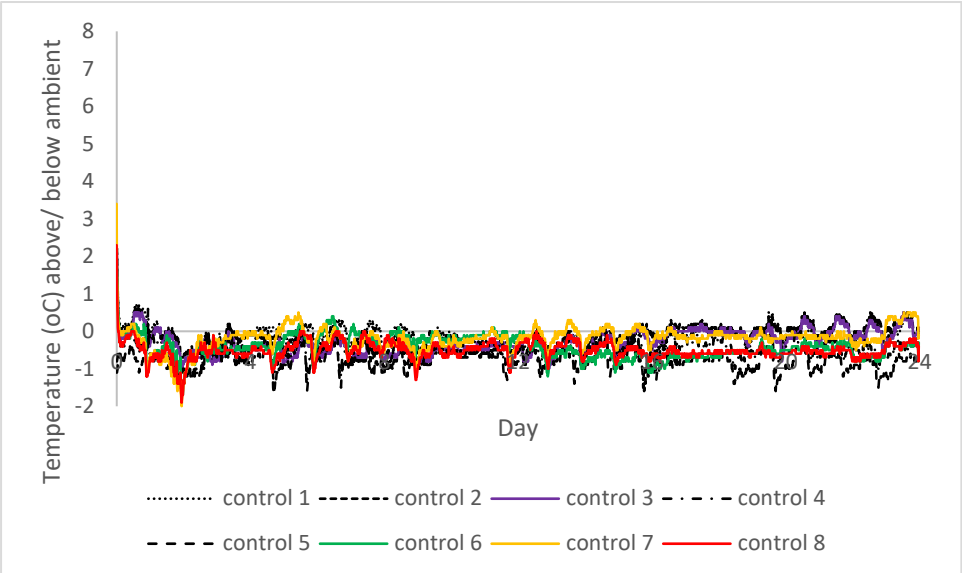

Temperature (oC) above/ below ambient
10
8
6
4
2
0
-2
0
4
12
16
20
24
28
Day
471
538
603

b



c

Fig. 5. The influence of the abundance of *Dermestes maculatus* larvae on abdominal temperature in decaying rats. (a) = zero dermestids; (b) = 50 adult dermestids at the start; (c) = 100 adult dermestids at the start. The numbers indicate the total number of larvae present on the body at the end of the observation period.



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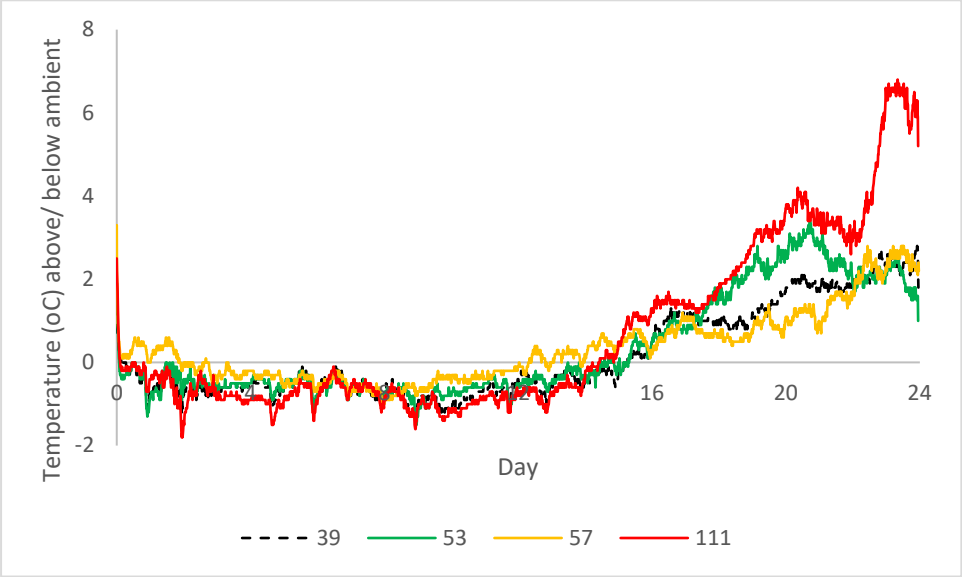
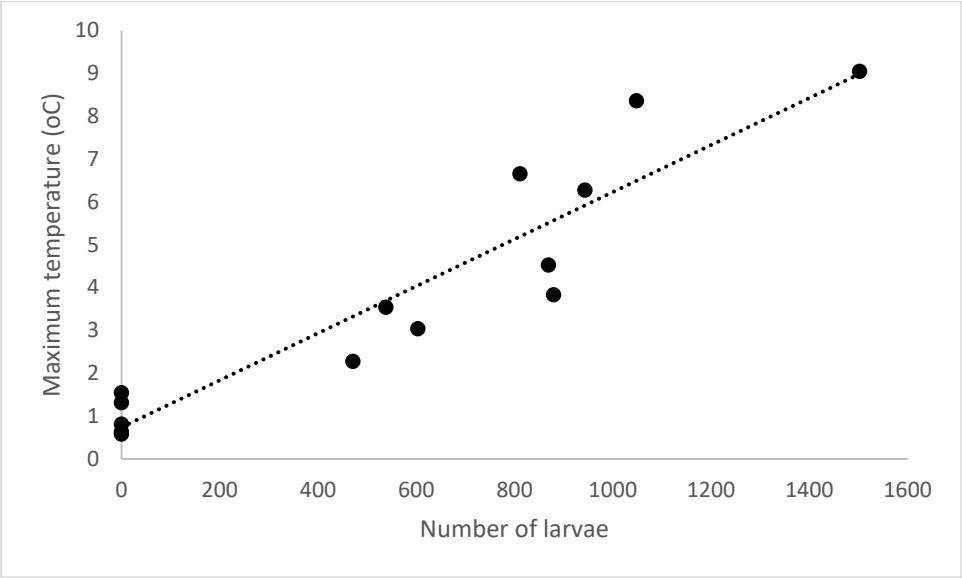


b

Fig. 6. The influence of the abundance of *Dermestes maculatus* larvae on abdominal temperature in decaying mice. (a) = zero dermestids; (b) = 20 adult dermestids at the start. The numbers indicate the total number of larvae present on the body at the end of the observation period.



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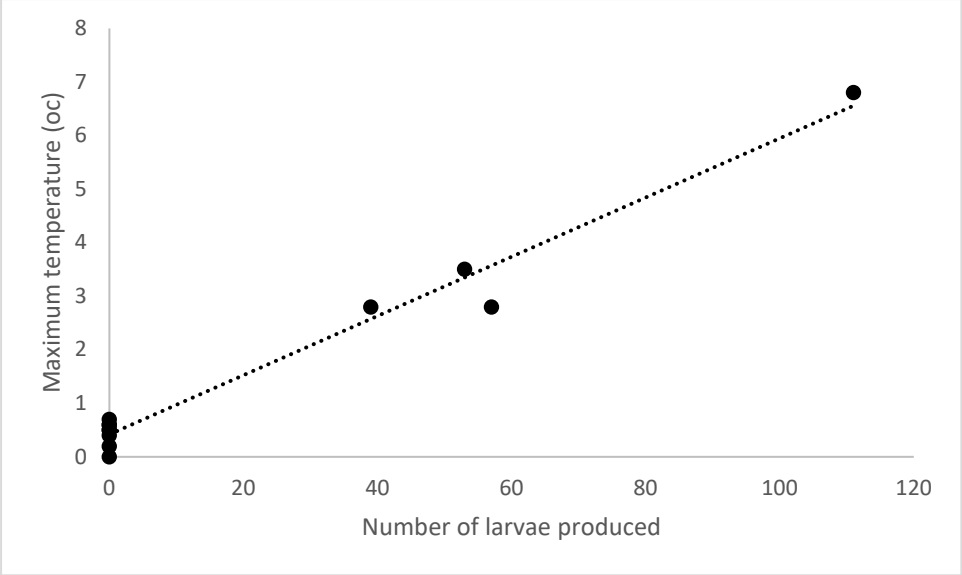

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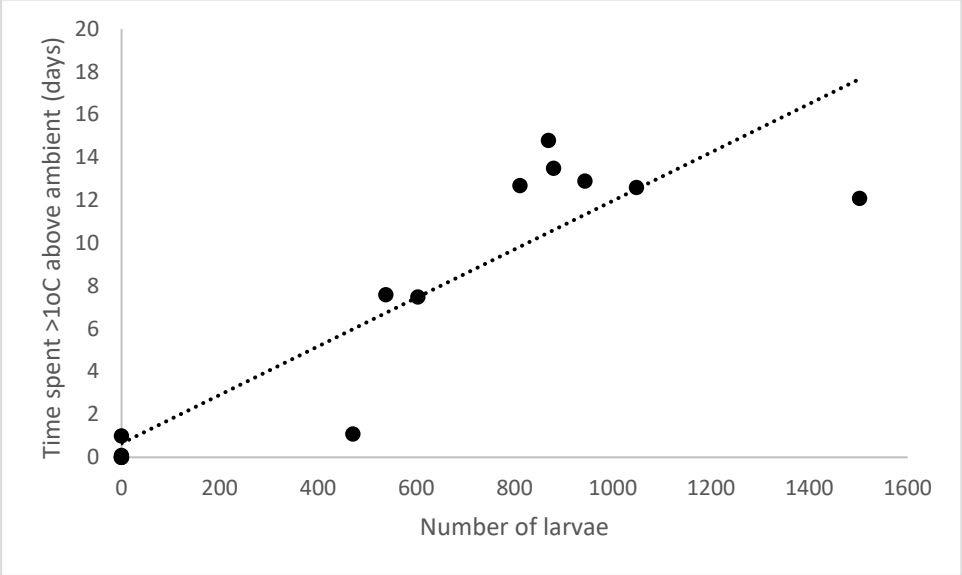
Fig. 7. The influence of number of *Dermestes maculatus* larvae produced on maximum abdominal temperature of decaying rats (a) and mice (b). Dotted line = linear trend line.



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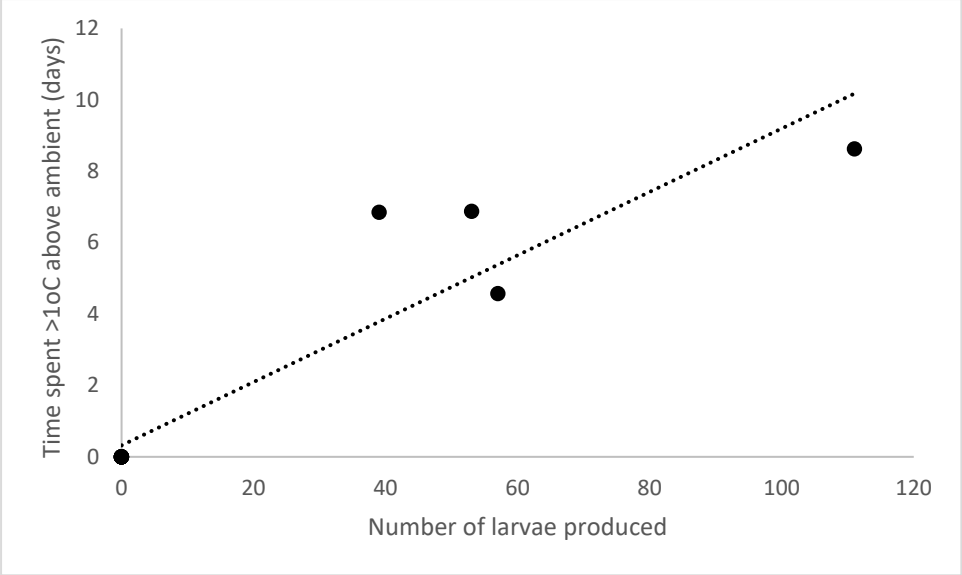
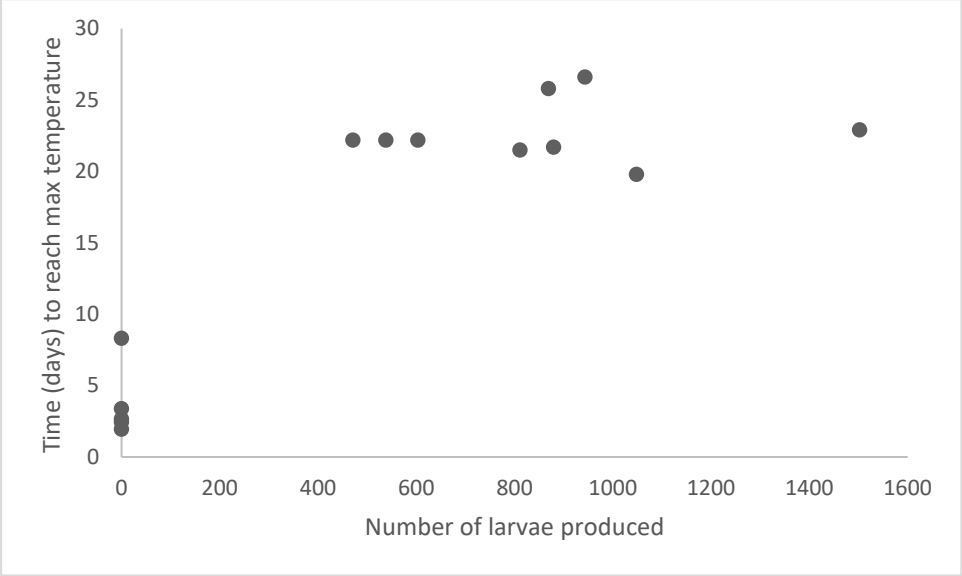


b

Fig. 8. The influence of number of *Dermestes maculatus* larvae on the duration with which the abdominal temperature of decaying rats (a) and mice (b) remains >1^{o}C above ambient. Dotted line = linear trend line.



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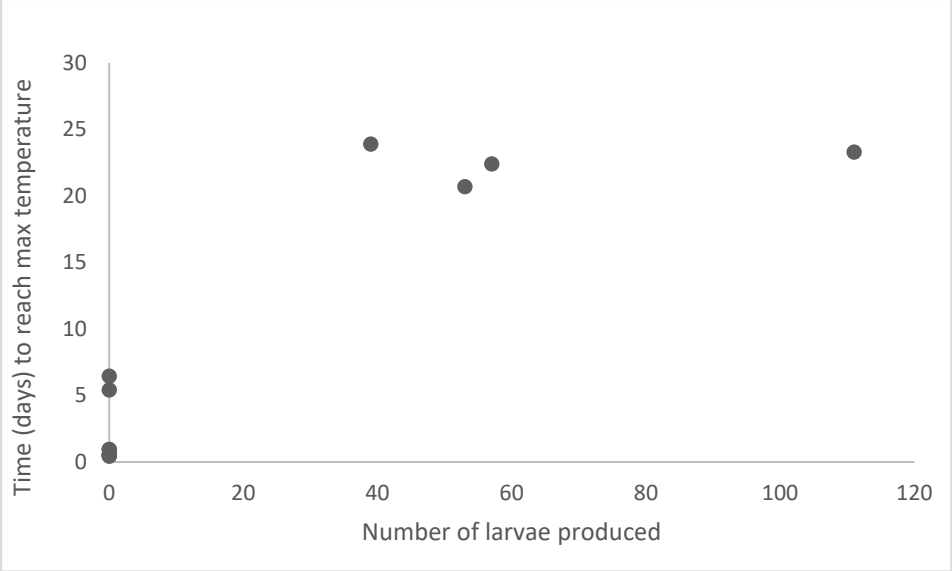

b

Fig. 9. The influence of fecundity of *Dermestes maculatus* on the time taken to reach maximum abdominal temperature of decaying rats (a) and mice (b).

4. Discussion

Dermestid beetles are most commonly encountered as pests of dried stored products [15] and in a forensic context they are usually associated with the colonisation of dry or mummified remains [4, 8, 16]. There are, however, reports of them being found on bodies at an earlier stage of decomposition [5, 17, 18]. Whilst acknowledging that adult beetles may appear at an early stage of decomposition, some forensic entomologists consider that their larvae are not found until the body has started to dry out [9, 19]. By contrast, the results described in this paper demonstrate that *Dermestes maculatus* can colonise bodies immediately after death and their larvae developed very quickly upon fresh remains. This is, perhaps, not surprising since there is a report of them causing deep wounds on live turkeys [20]. The insects are therefore willing and able to feed on moist flesh. Female beetles oviposited directly into the skin particularly above the muscular parts of the body and less so on the feet or forelegs. This would accord with the observation that on stored products the females prefer to oviposit onto muscle rather than fat or bone marrow on which the larvae grow more slowly [21]. Direct oviposition into muscles of dried fish has also been described [22] although some workers state that the females oviposit

underneath or near to the larval food source rather than upon it [6]. Presumably, some of the variability will depend upon the nature of the food and that of the surrounding substrate. In contrast to the sequence of colonisation and consumption observed in these experiments, on humans it is the head, hands, and feet of human corpses that are first consumed by dermestids and the chest is one of the last regions to be skeletonised [3]. This is probably a consequence of the very big differences in sizes of rodents and humans and therefore of the amount of food and physical challenges that the different parts of the body present. However, the abdominal cavity of human corpses infested by dermestids is also reduced to a 'light brown humus' [3].

The lack of reports of dermestid beetles from fresh remains may be largely a consequence of them being outcompeted at this stage of decomposition by blowflies and other more mobile, less temperature sensitive and more rapidly reproducing species. This would therefore be an example of the difference between fundamental and realised ecological niche, *sensu* Hutchinson [23]. Although dermestid beetles are often associated with dry remains, low humidity can compromise their growth and reproduction. For example, Katz et al. [24] found that *D. maculatus* larvae developed to pupation within an average of 36.2 days at 65% relative humidity (r.h.) but took an average of 55.8 days at 35% r.h.. The results of the present experiments indicates that the larvae can develop even faster when they are feeding on fresh remains and this may be further facilitated by thermogenesis associated with masses of larvae feeding in close proximity. In addition to feeding on dry animal products, *Dermestes ater* (De Geer) also preys on the larvae and pupae of *Musca domestica* [25] and whilst it is likely that *D. maculatus* would exhibit similar predatory activity (it is certainly cannibalistic) it is not known whether it would affect the colonisation of remains by other insect species.

Although dermestid adults and larvae are adapted for feeding on dry materials, they did not avoid moist tissues and the eyes were among the first tissues consumed whilst the tail was often one of the last tissues to be skeletonised. The author's unpublished observations indicate that the eyes of recently killed birds and other vertebrates are also quickly located and consumed by *D. maculatus*. *Dermestes maculatus* modify experimental post-mortem wounds in pigs' trotters [17] and it is therefore likely that they will do the same with fresh wounds. A characteristic feature of adult dermestids is the production of long thin dry frass contained within a peritrophic membrane and this has been used as a forensic indicator [26]. However, in

the work described in this paper those feeding on moist flesh always produced faeces in the form of short moist flecks.

The negative correlation between the duration of the bloat stage of decomposition in rats and the number of larvae produced indicates that they play an important role in the speed of decay from an early age. Clearly, the number of larvae present on the rats at the end of the bloat stage will be lower than the final number because eggs are laid throughout the decay period (as indicated by the presence of recently hatched larvae at the end of the experiments). However, by day 28 on the rats, the majority of larvae were large and some were starting to pupate. This indicates that in this study those eggs laid during the first few days of the decay period were most likely to complete their development. This would probably be at least partly a consequence of the adults inserting eggs beneath the skin of the dead animal. As the dermestid population grew and the dead body was consumed, there would be an increasing probability of eggs being eaten before they hatched.

The starting densities of the adult dermestids on rats did not affect the number of larvae produced per adult. This, obviously, is a crude measure of fecundity because the proportion of male: female adults, their ages, and reproductive status were not controlled. However, because a large number of insects were used and the same random factors were applied to all treatments this probably did not unduly affect the results and the situation was similar to that which would affect the colonisation of a dead body in a crime scene scenario. It also suggests that for the duration of the experiments, the insects did not suffer undue competition. By contrast, the fecundity of the beetles on mice was much lower than on rats. It is possible that this was because there was relatively less food available per beetle but if this was the case the mice would have become skeletonised even faster. It is more likely that the larger surface area: volume ratio of the mice resulted in them drying out more rapidly. Consequently, the adult dermestids and their larvae had to consume relatively dry remains that were not as easy to chew and metabolise as the fresh rat tissue. The smaller body size may also have facilitated cannibalism of the eggs and young larvae.

The rise in abdominal temperature at the end of the decomposition period only occurred when dermestid beetles were present. Furthermore, the maximum temperature and the duration over which the temperature was more than $1^{o}C$ above ambient were correlated with the beetles' fecundity. There was little change in the temperature of the controls throughout the experiment. Indeed, for most of the time,

in both the controls and the experimental rats and mice, the temperature was at or slightly below ambient. The below ambient temperatures probably resulted from evaporative cooling. There was no increase in temperature associated with the bloat stage of decomposition when there is pronounced microbial decomposition in the abdominal region (and elsewhere) which suggests that the subsequent rise was not solely a consequence of microbial activity. Instead, the rise would appear linked to the exposure and consumption of the viscera by the dermestids. By the time the abdominal cavity was exposed, the viscera were reduced to a thick brown paste. Any rise in temperature, and in particular the length of time it remains above ambient, will almost certainly speed up larval dermestid development. Blowfly maggot feeding masses are well-known for their ability to cause a localised increase in temperature that may exceed 20^{o}C above ambient [27]. In this case, the rise in temperature is determined by a combination of the larval instar, the amount of food present, the volume of the maggot feeding mass and the temperature and heat transfer characteristics of the surrounding medium (e.g. whether the body is found on dry warm soil or cold wet concrete) [28]. The temperature rise associated with maggot feeding masses typically has a single peak and is associated with large numbers of larvae reaching the late 2nd/ early 3rd instar. The actual cause of the rise has been attributed to 'exothermic digestive processes' [29], although precisely what these are remains uncertain. It has also been suggested that large numbers of maggots could promote aerobic bacterial decomposition which is more thermogenic than anaerobic decomposition [30]. It is probable that the dermestid larvae have a similar effect when feeding on rats and mice. That is, the exposure of the viscera coupled with the physical churning of the remains by the larvae facilitates the access of oxygen and therefore aerobic microbial decomposition. If the temperature probe is inserted into the thorax then a similar increase in temperature is found associated with the feeding of large numbers of dermestid larvae in this region (unpublished obs.). Whether the dermestid larvae have a direct influence on the rise in temperature (rather than through stimulating microbial growth) awaits further study.

5. Conclusion

The data indicate that *Dermestes maculatus* will feed and oviposit upon dead bodies that are less than 1 hour old. They can complete their larval development on a fresh body and rapidly skeletonise it in the process. There is a localised increase in

abdominal temperature associated with the exposure and consumption of the viscera by larval dermestids. The rise in temperature and its duration correlates with the number of larvae present.

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