EFFECT OF LARVAL SECRETIONS AND EXCRETION ON SELECTION OF FOOD SOURCE BY *DERMESTES MACULATUS* DEGEER

An Undergraduate Research Scholars Thesis

by

ANN R. GEORGE

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ABSTRACT

Effect of Larval Secretions and Excretion on Selection of Food Source by
Dermestes maculatus DeGeer

Ann George
Department of Biomedical Science
Texas A&M University

Research Advisor: Dr. Jeffery Tomberlin
Department of Entomology
Texas A&M University

Thesis

Some preference by adult *D. maculatus* will be shown for the dog food not treated with intraspecific larval secretion/excretion product.

Theoretical Framework

Insect secretions and excretions produced by larval *D. maculatus* associated with a potential food source of adults produce volatiles, which ultimately impact the decision of competing adult beetles to utilize, or not, the resource in question. Determining the impact of larval secretions and excretion on the decision-making process of *D. maculatus* will provide insight into the mechanisms behind necrophagous insect succession on vertebrate carrion.

Project Description

Necrophagous insects utilize cues such as volatiles and compounds in the environment, collectively known as public information, while locating ephemeral resources such as a decaying corpse. Volatiles, including those emitted from competing individuals, inform an organism's decision to colonize or avoid certain food sources and are thus critical triggers for insect

colonization and succession. This study seeks to determine if and to what extent larval secretions and excretion affect the resource selection process of *Dermestes maculatus,* a local necrophagous species. Adult beetles were allowed to make a choice between dog food treated with larval secretions and excretion collected from *D. maculatus* larvae, and untreated dog food. Preference for untreated food would indicate that compounds present in larval excretions and secretions may serve as compelling indices of the presence of a competing colony. Determining the impact of larval secretions and excretion on the decision-making process *of D. maculatus* will provide insight into the mechanisms behind necrophagous insect succession.

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KEY WORDS

PMI	Post Mortem Interval
minPMI	Minimum Post Mortem Interval
SE	Secretion/ Excretion
VOC	Volatile Organic Compound
D/D	Deionized/Distilled

CHAPTER I

INTRODUCTION

Insects in forensic investigations

Forensic entomology is the name given to the application of the study of insects to investigations associated with legal matters. (Keh 1985). Lord & Stevenson (1986) subdivided this science is in three categories: urban, stored products and medico-legal. Medico-legal entomology, also known as medico-criminal entomology, studies the arthropods associated with violent crimes (Hall 1990). The main objective of medico-legal entomology is the estimation of the postmortem interval (PMI), defined as the interval between the death and discovery of the body (Catts & Goff 1992). Insect development and succession has been shown to be reliably predictable and correlated with environmental factors such as climate (Smith 1986). Thus, species present on remains can be used to entomologically estimate PMI, often using one or a combination of two methods. The first method entails raising sample specimens of insect species colonizing a body to maturity and comparing this time interval with known developmental times to estimate a timeframe for colonization based on the conditions of the environment and the body (Catts and Goff 1992). This information can be used to establish a minimum PMI (minPMI). MinPMI can also be estimated by creating a successional timeline based on species collected on a corpse and succession tables and colonization timeframes generated by controlled studies (Catts 1990; Goff & Flynn 1991; Tabor et al. 2004).

The applicability of Coleoptera in minPMI estimation is usually restricted to patterns found in successional studies in animal models (Kulshrestha & Satpathy 2001). Coleopterans, including those belonging to the family Dermestidae, are generally found during the advanced stages of decomposition and therefore tend to have a secondary role in forensic entomology (Archer et al. 2005, Kulshrestha & Satpathy 2001). Emphasis has traditionally been placed on species quicker to arrive at sites of decay, such as those belonging to the Dipteran families Calliphoridae and Sarcophagidae (Kulshrestha & Satpathy 2001, Tabor et al. 2004, Tabor et al. 2005). Consequently, data concerning late stage decomposers, such as dermestids, is less accurate and harder to find than that of early colonizers (Archer et al. 2005, Magni et al. 2015). Numerous records of forensic cases involving mummified or skeletonized remains in late stages of decomposition underline the value of accurate and nuanced understanding of the development and succession of late colonizing insects (Charabidze et al. 2013, Magni et al. 2015). Patterns of insect succession are driven by environmental cues such as volatile emissions from microbial populations, factors in the environment, and compounds and cues produced by other insect species (Davis et al. 2013, Magni et al. 2015, Paczkowski et al. 2014, von Hoermann et al. 2011). These cues, collectively part of the public information an organism uses to make decisions, inform the organism of the presence and availability of a resource (Catts & Goff 1992; Joseph et al. 2011). Analysis of the compounds released by both a decomposing corpse and the species present on it over time should allow investigators to construct a reasonably accurate timeline of succession for a corpse if it is known how certain species respond to specific environmental cues.

Relevance of Dermestidae and *Dermestes maculatus* DeGeer

Due their presence on corpses in the Forensic Anthropology Research Facility (FARF) in Texas State's Freeman Ranch, *Dermestes maculatus* DeGeer beetles were used for this study. *D. maculatus* is a cosmopolitan species with records in several papers (Archer & Elgar 1998, Richardson & Goff 2001, Schroeder et al. 2002). Primarily known as an urban pest species, *D. maculatus* is widely documented as a common dry stage decomposer (Bruesch 2011, Magni et al. 2015). Dermestidae are commonly associated with remains in relatively arid environments and are often the only insect species present in extreme dry environments such as desert (Magni et al. 2015). Unlike some other necrophagous species of Dermestidae, *D. maculatus* has been known to consume moist remains and dead insects as well as prey on larvae of other necrophagous species (Braak 1987, Magni et al. 2015).

A study by Shean, Messinger & Papworth (1993) on insect succession on shaded and exposed pig carcasses found dermestid species on exposed remains during later stages of decomposition and no dermestids on shaded remains for the duration of the study. The experiment suggests that colonization and succession of dermestids depends on environmental factors. Environmental factors may include state of succession on a resource. Colonization by other species can inhibit or facilitate Dermestidae resource selection, a phenomenon known as priority effects (Magni et al. 2015). Charabidze et al.'s (2013) compilation of case studies in France suggests the potential of intraspecific competition between dermestids and other necrophagous insects due to the former's prevalence in indoor cases over outdoor cases. The study also noted that generally only a single species of Dermestidae was present in a death scene, indicating the possibility of competitive exclusion of other dermestid species (Charabidze et al. 2013). Therefore, it is likely the presence of other insects impacts Dermestidae colonization.

Intraspecific Interactions and Colonization by *Dermestes maculatus* DeGeer

While the impact of interspecific competition on resource selection by *D. maculatus* has several studies dedicated to the topic, intraspecific competition is referenced in relatively few papers and generally in the context of established colonies (Archer and Elgar 1998, Charabidze et al. 2013, Magni et al. 2015, Richardson & Goff 2001). Literature on interactions between individuals focus on adult-to-adult or inter-larval communications (Archer & Elgar 1998, Hoermann et al. 2012, Levinson et al. 1980, Richardson & Goff 2001, Shaaya 1981). Although adult aggregation factors serve as attractants to larvae, no data exist on adult responses to larvae-produced compounds (Rakowsi & Cymborowski 1981). While *D. maculatus* adults have been shown to pick up cues from other adults by way of sex pheromones and aggregants in adult feces, responses of resource-seeking adults to larvae from colonized resource have not been the focus of any studies (Hoermann et al. 2012, Levinson et al. 1980, Shaaya 1981). Intraspecific competition and impact of food resource availability has been observed in larvae within a colony in several papers (Archer & Elgar 1998, Richardson & Goff 2001, Woodcock *et al.* 2013). Density-dependent studies of *D. maculatus* larvae by Richardson & Goff (2001) present a slight negative correlation between increasing density and survivorship, suggesting that intraspecific competition may contribute to larval mortality. Factors contributing to decreased survivorship may include lack of suitable pupation sites (Archer & Elgar 1998). Larvae without pupation sites are subject to cannibalization as exposed pupae and delay pupation, which leads to reduced adult body mass and heightened disease risk (Archer & Elgar 1998). In their developmental studies, Richardson & Goff (2001) also observed cannibalization of eggs by early-hatching larvae.

Given the evidence of competition between larvae on the same resource, it is possible that the presence of larvae may serve as a deterrent to adults seeking to colonize a food resource and mate with adults already present. Once a few individuals have been recruited to remains, adult beetles release sex pheromones, aggregate quickly, and begin mating (Schroeder et al. 2002, von Hoermann et al. 2012). Whether this aggregation continues at the same rate after laying of eggs and growth of larvae is unclear from available literature. Isolation and utilization of larval SE product, a source of larvae-derived semiochemicals, could provide insight on how adults perception of larvae from another colony of the same species inform resource selection by the former.

CHAPTER II

MATERIALS AND METHODS

Lab Colony

Dermestes maculatus reared in colony by the Texas A&M's F.L.I.E.S. Facility were used in this experiment. This colony was established in August of 2015 from adults and larvae found on site at the Forensic Anthropology Research Facility (FARF) in Texas State's Freeman Ranch. The colony is kept at 30°C, 12:12 L:D cycle at 50% relative humidity. Adult beetles used in this experiment were collected as pupae and reared individually for the duration of experimentation.

Secretion/Excretion Collection

Larvae from eggs hatched on the same day were raised on a dog food diet separate from the main colony. Prepupal larvae about 10-15 mm in length were collected once prepupal burrowing was observed. Collected larvae were placed five to a tube in 15 mL Falcon tubes with 1mL of deionized distilled water (Figure 1). The tubes were placed on their sides to allow larvae to walk freely, and incubated for 1 hr at 30°C. Larvae were removed from the Falcon tubes and the resulting SE product was collected and stored in 15 mL Falcon tubes at 0°C.

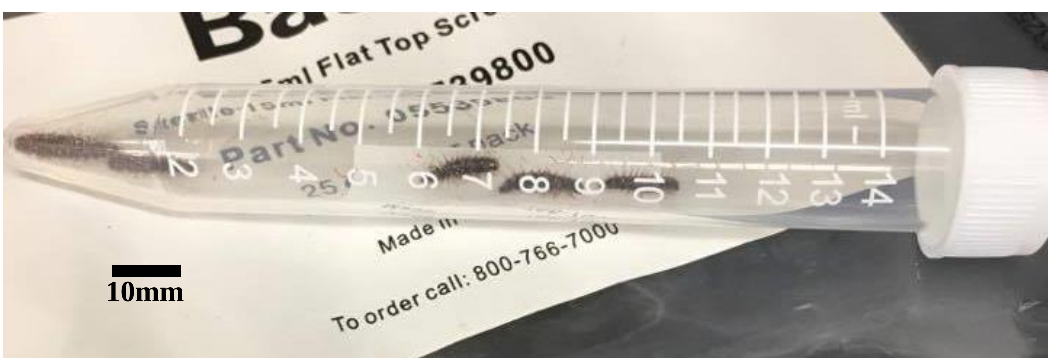

Figure 1. 15 mL Falcon tube with 1 mL D/D water and five prepupal *D. maculatus* larvae, as used for SE product collection.

Behavior Experiment

Setup

Figure 2: Y-tube System used in Pilot Two behavior experiments. A single *D. maculatus* adult was introduced into the front-facing introduction tube, which was then sealed with parafilm. Dog food treated with either SE product or DD water were placed in the containers at the ends of the Y-tube arms. Adults were left in the Y-tubes for 24 hr.

All trials were run in complete darkness in a sealed room set at 28°C. Y-tubes were constructed from clear PVC pipes and fitted with plastic containers on each side (Figure 2). The treated or control dog food was placed in these containers. The entry tube measured 30.5 cm from mouth to joint and both arms measured 61 cm from joint to opening of food containers. Upon introducing an adult into the Y-tube, parafilm was placed over the mouth of the introduction tube to seal the Y-tube. Beetles were permitted to freely move from one side of the Y-tube to the other.

Data Collection

Beneful® Originals beef dog food was treated with 1 mL of either deionized distilled water or SE product and left for 1 hr prior to experimentation. For the experiments, 50 g of SE treated dog food were placed in one side of the Y-tube. For the control, 50 g of dog food treated with only D/D water were placed in the other side of the Y-tube. Sides for treatment and control were randomly determined. A single, randomly selected adult beetle was introduced into each Y-tube and allowed to move freely. Beetle positions in the Y-tubes were recorded 24 hr after placing them in the Y-tubes. Location of the treatment/control dog food in the y-tube and beetle sex/identity was also recorded.

CHAPTER III

RESULTS

Pilot Trials

This study evaluated adult preferences between food treated with larval SE product or food treated with D/D water. Pilot experiments were run to develop a method to maximize response.

Pilot One: Longer Introduction Tube

Virgin adults were sent through the system described in the methods with the exception of a 61 cm introduction tube.

Trial	Age of Beetles	No Response	Treatment	Control
1	4 days	5	0	0
2	8 days	5	0	0
3	14 days	3	2	0
4	30 days	2	1	2

Table 1. Age and number of adult *D. maculatus* displaying a preference in Pilot 1 behavior experiment. Resource preference was indicated by beetle presence in the corresponding Y-Tube arm at the end of 24 hr. Beetles in the introduction tube or joint after 24 hr were marked “No Response.”

Pilot Two: Shortened Introduction Tube

Because individuals in previous pilot trials were observed some distance down the introduction tube at the end of the 24 hr period, the introduction tube was shortened in an attempt to force a decision by beetles already willing to move down the tube. Virgin beetles were sent down introduction tubes 30.5 cm in length.

Trial	Age of Beetles	No Response	Treatment	Control
1	4 days	5	0	0
2	6 days	4	0	1
3	24 days	2	2	1
4	32 days	1	2	2

Table 2. Age and number of adult *D. maculatus* displaying a preference in Pilot 2 behavior experiment. Resource preference was indicated by beetle presence in the corresponding Y-Tube arm at the end of 24 hr. Beetles in the introduction tube or joint after 24 hr were marked "No Response."

Analysis of Pilot Studies

Results of the two pilot studies were plotted against the age of beetles in Figures 3 and 4. In both studies, response appears to increase with age.

Pilot Study 1 displayed 25.0% response across all trials. In beetles aged less than 2 wk, percent response was 0.0%. In beetles aged between 2-5 wk, percent response was 50.0%. Among those responding, 40.0% chose the SE treated resource and 60.0% chose the D/D water treated resource.

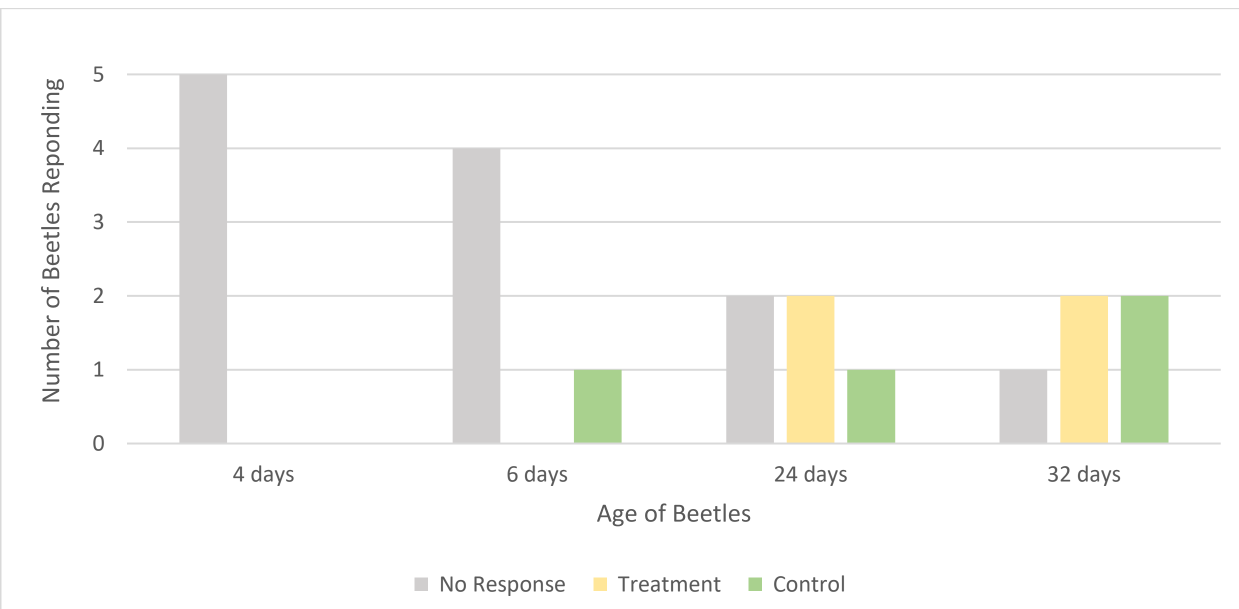

Figure 3. Number of *D. maculatus* adults preferring SE treatment or D/D water control, or failing to respond in Pilot Study 1 behavior experiment, according to age of beetles tested.

Pilot Study 2 appeared to demonstrate an increased percent response, although the significance of this increase cannot be established due to irregularities between the two studies. 40% of beetles in all trials made a decision. In beetles aged less than 1 wk, percent response was 10%. In beetles aged between 3-4 wk, percent response was 70%. Out of those that responded among both groupings, 57.1% chose the SE treated resource and 42.9% chose the D/D water treated resource.

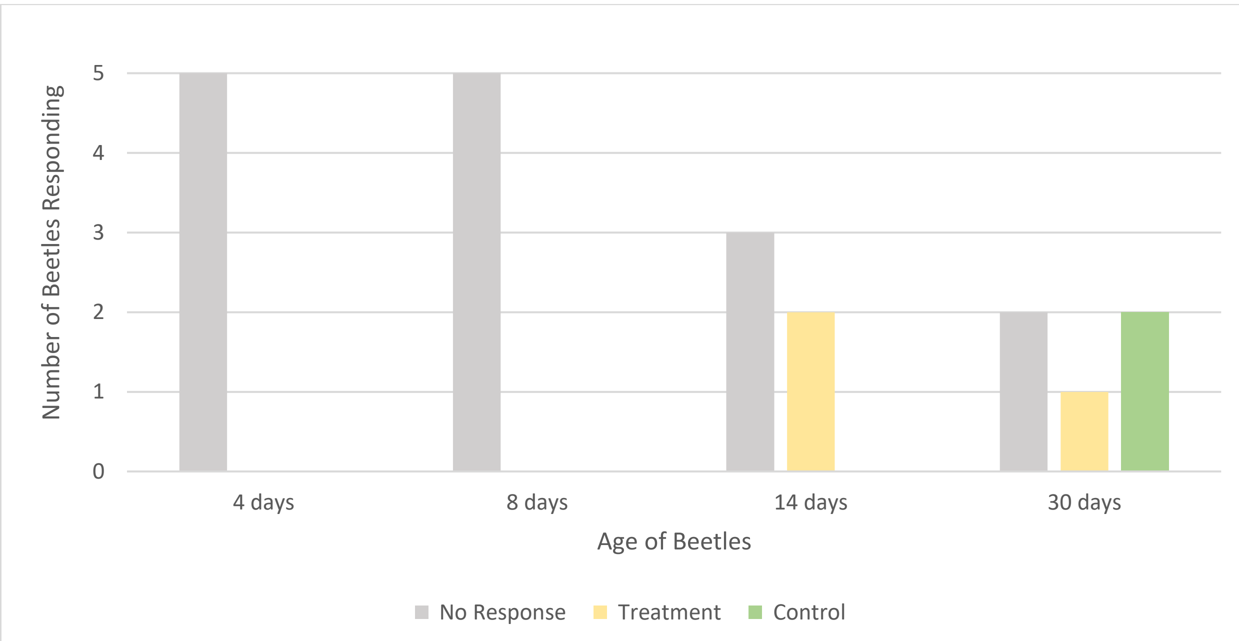

Figure 4. Number of *D. maculatus* adults preferring SE treatment or D/D water control, or failing to respond in Pilot Study 2 behavior experiment, according to age of beetles tested.

Pilot studies demonstrated an increase in percent response in adults around 2 wk old. Response appeared to become indiscriminate in beetles older than 3 wk.

CHAPTER IV

DISCUSSION

Findings from Studies

Development of this study indicated several patterns to adult behavior. Decision making increased as beetles aged although it lacked specificity in beetles 30-32 days old. Young virgin adult beetles within ten days of their eclosion date showed a very low percent response of approximately 5% across all pilot studies. 60% of beetles aged two weeks and older chose a resource. Selection by the individuals that responded narrowly favored SE product-treated food. The significance of these results cannot be established based on the limited data; thus, the hypothesis of this study cannot be rejected. However, trends indicated by the experimental data bear investigating.

Secretion-Excretion Product as a Potential Attractant

Dermestids, including *D. maculatus,* are aggregate feeders, colonizing a resource with multiple individuals of the same species in close proximity to each other and their offspring (McNamara et al. 2008, Rakowski 1988, Rakowski & Cymborowski 1986). In adults, the combination of sex pheromones and aggregation factors found in feces attracts adults to each other (Levinson et al. 1980, Rakowski & Cymborowski 1982, Rakowski & Cymborowski 1986). Larvae also secrete aggregation factors, which, along with adult aggregation factors, draw them to other individuals (Rakowski & Cymborowski 1982). Adult factors translate across developmental stages, but produce different effects (McNamara et al 2008, Rakowski & Cymborowski 1986). Rakowski and Cymborowski (1986) demonstrated that larval aggregation factor appeared to accelerate larval growth, but larvae exposed to only adult aggregation factor experienced more synchronized ecdyses, increased body mass, and protracted larval development compared to control groups. Adults may view other larvae as beneficial to potential offspring rather than competition for resources for the beneficial effect of larval aggregation factor has on larval development. Density-dependent studies by Richardson & Goff (2001) and Rakowski and Cymborowski (1982) indicated an optimal larval density which resulted in accelerated development and increased larval body mass. At concentrations reflecting optimal density, larval SE product could indicate a supportive environment for potential offspring. Due to the species preference for aggregate feeding, adults are generally found among larvae (Fontenot et al. 2015, Jones 2006, Rakowski & Cymborowski 1982). Presence of larvae may cue single adult beetles to the presence of other adults. Other adults serve as potential mates as well as promoters of healthy, synchronized larval development (Fontenot et al. 2015, Rąkowski, & Cymborowski 1982). To the extent of available literature, *D. maculatus* attraction to resources is driven by sex pheromones produced by the opposite sex, aggregation factors in adult feces, and, in the case of males, certain carrion odors (Hoermann et al. 2012, Levinson et al. 1980, McNamara et al. 2004, Rąkowski, & Cymborowski 1986, Shaaya 1981). Hoermann et al. (2012) demonstrated that adult females responded negligibly to carrion odors. Females display a stronger response to adult aggregation factors than males (Jaskulska et al. 1987, von Hoermann et al. 2012). It is possible that females are attracted to larval secretions and excretion due to their dependence on semiochemicals produced by other individuals of the species. Larval presence may indicate a suitable resource and an environment supportive of successful larval development.

Other factors that may contribute to adult preference for SE product-treated food include the nature of the carrion resource preferred by *D. maculatus*. Compared to earlier stages of decomposition, which can vary greatly in duration according to conditions of the environment, dry and skeletal remains can exist for extremely prolonged periods of time (Catts & Goff 1992, Charabidze et al. 2013, Magni et al. 2015). For late-stage decomposers, availability of dried carrion is not significantly limited by natural progression of decay (Charabidze et al. 2013, Magni et al. 2015). The ephemerality of D. maculatus' resource is reduced in comparison to organisms requiring fresh or moderately decayed remains (Catts and Goff 1992, Kulshrestha & Satpathy 2001). Intraspecific competition may not be as large a factor in resource selection for D. maculatus as to early-colonizers such as dipterans (Kulshrestha & Satpathy 2001). A final factor of importance is the SE product used in this experiment, which was collected from prepupal larvae. Prepupal larvae generally do not feed and therefore may not serve as indicators of a competitive presence to potential offspring of resource-seeking adults (Archer et al. 1998, Richardson & Goff 2001).

Beetle Age and Responsivity and Selectivity

The impact of age in responsivity in behavior has been documented in sex pheromone and aggregation factor research on *D. maculatus*. Response to female sex pheromone by male beetles in a study by Abdel-Kader and Barak (1978) increased with age in adults 0-14 d post-eclosure.also demonstrated that response to sex pheromones as well as the presence of other adults increased with age in beetles 0-6 d post-eclosure (Shaaya 1901). However, adult response to adult aggregation pheromone was shown by Rakowski & Cymborowski (1986) to decrease with age. *D. maculatus'* response to semiochemicals appears to be age dependent, though response does not always positively correlate with age. In the case of compounds in larval secretions and excretions, responsivity does appear to increase with age. Selectivity in insects generally decreases with age as mortality risk and sensory capability diminish (Alder & Bobduiansky 2014). It is possible that the reduced selectivity observed in older adults can be correlated to age.

CHAPTER V

FUTURE DIRECTIONS

Pilot studies indicated a potential preference for SE treated food in beetles around 2-3 weeks old. More extensive testing is needed to support this observation. Additional replicates at a range of ages between 1-5 wk are necessary to confirm the decline in selectivity after 3 weeks of age and lack of response in newly eclosed beetles.

The SE product was collected from only five larvae for every 1 mL of water; a colonized resource might have hundreds of larvae. Recreating this study with a more concentrated SE product made with greater numbers of larvae may produce a different or more pronounced response in the adult beetles and more faithfully demonstrate response in natural environments.

Analysis of the VOCs produced in the larval SE product by collection and gas chromatography should yield the identity of specific compounds present in the SE product. Identification of these VOCs could isolate the compounds used as cues for behavior.

This study sought to explore the effects of *D. maculatus* larval secretions and excretion on resource selection by adults of the species. Upon completion of experimentation, the findings in this study could hold implications for the mechanisms behind *D. maculatus'* utilization of volatile organic compounds in their search for ephemeral resources.

WORKS CITED

Abdel-Kader, M. M. and A. V. Barak. 1979. Evidence for a sex pheromone in the hide beetle, *Dermestes maculatus* (De Geer) (Coleoptera: Dermestidae). **Journal of Chemical Ecology 5**: 805-813.

Archer M. S. & M. A. Elgar. 1998. Cannibalism and delayed pupation in hide beetles, *Dermestes maculatus* DeGeer (Coleoptera: Dermestidae). **Austral Entomology 37**: 158-161.

Archer M. S., R. B. Bassed, C. A. Briggs & M. J. Lynch. 2005. Social isolation and delayed discovery of bodies in houses: The value of forensic pathology, anthropology, odontology and entomology in the medico-legal investigation. **Forensic Science International 151**: 259–265.

Braak L.E.O. 1987. Community dynamics of carrion-attendant arthropods in tropical African woodland. **Oecologia 72**: 402–409.

Bruesch J. 2011. Fabric and museum pests, pp. 680–734. In: Mallis A. (ed.), **Handbook of pest control. The behavior, life history, and control of household pests**, 10 ed. The Mallis Handbook Company, G.I.E. Pub, OH. 1600 p.

Catts, E. P. 1990. Analyzing entomological data, p. 124-137. *In*: Catts, E. P. & N. H. Haskell (eds.). **Entomology & Death: A Procedual Guide.** Clemson: Joyce's Print Shop. xii+182 p.

Catts, E. P. & M. L. Goff. 1992. Forensic entomology in criminal investigations. **Annual Review of Entomology 37:** 253-272.

Charabidze, D., T. Colard, B. Vincent, T. Pasquerault & V. Hedouin. 2013. Involvement of larder beetles (Coleoptera: Dermestidae) on human cadavers: A review of 81 forensic cases. **International Journal of Legal Medicine 128**: 1021–1030.

Davis, T. S., T. L. Crippen, R. W. Hofstetter & J. K. Tomberlin. Microbial volatile emissions as insect semiochemicals. **Journal of Chemical Ecology 39**: 840-859.

Goff, M. L. & M. M. Flynn. 1991. Determination of postmortem interval by arthropod succession: a case study from the Hawaiian Islands. **Journal of Forensic Sciences 36:** 607-614.

Hall, R. D. 1990. Medicocriminal entomology. In: Catts, E. P.; N. H. Haskell (eds.) **Entomology & death: A procedual guide**. Clemson: Joyce's Print Shop. 180 p.

Jaskulska, B., G. Rakowski & B. Cymborowski. 1987. The effect of juvenile hormone on aggregative behaviour of Dermestes maculatus. **Comparative Biochemistry and Physiology Part A: Physiology 87**: 771-773.

Jones, T.M. & M. A. Elgar. 2004. The role of male age, sperm age and mating history on fecundity and fertilization success in the hide beetle. **Proceedings of the Royal Society of London, Series B: Biological Sciences 271**: 1311-1318.

Jones, T. M., K. B. McNamara, P. G. R. Colvin, R. Featherston & M. A. Elgar. 2006. Mating frequency, fecundity and fertilization success in the Hide Beetle, *Dermestes maculatus*. **Journal of Insect Behaviour 19**: 357–371.

Joseph I., D. G. Mathew, P. Sathyan & G. Vargheese. The use of insects in forensic investigations: An overview on the scope of forensic entomology**. Journal of Forensic Dental Sciences 3.2**: 89-91.

Keh, B. 1985. Scope and applications of forensic entomology. **Annual Review of Entomology 30:** 137-54.

Kulshrestha, P. & D. K. Satpathy, 2001. Use of beetles in forensic entomology. **Forensic Science International 120**: 15-17.

Levinson, H. Z., A. R. Levinson & W. Francke. Feeding aggregants in the faeces of *Dermestes maculatus* DeGeer. 1980. **Die Naturwissenschaften 67**: 643–645.

Lord, W.D. & J.R. Stevenson. 1986. **Directory of forensic entomologists**, 2nd. Ed. Def. Pest. Mgmt. Info. Anal. Center, Walter Reed Army Medical Center, Washington, D.C. 42 p.

Magni, P.A., S.C. Voss, R. Testi, M. Borrini & I.R. Dadour. 2015. A biological and procedural review of forensically significant *Dermestes* species (Coleoptera: Dermestidae). **Journal of Medical Entomology 52**: 775-769.

McNamara, K.B., R. L. Brown, M. A. Elgar & T. M. Jones. 2008. Paternity costs from polyandry compensated by increased fecundity in the hide beetle. **Behavioral Ecology 19**: 433-440.

McNamara, K. B., T.M. Jones & M.A. Elgar. 2004. Female reproductive status and mate choice in the hide beetle, Dermestes maculatus. **Journal of Insect Behaviour 17**: 337–352

Paczkowski, S., S. Nicke, H. Ziegenhagen & S. Schutz. 2015. Volatile emission of decomposing pig carcasses (*Sus scrofa domesticus* L.) and an indicator for the postmortem interval. **Journal of Forensic Sciences 60**: 130-137.

Rąkowski, G. & B. Cymborowski. 1981. Aggregation pheromone in *Dermestes maculatus*: effects on larval growth and developmental rhythms**." International Journal of Invertebrate Reproduction 4.4**: 249-254.

Rąkowski, G. & B. Cymborowski. 1986. Some environmental and physiological factors influencing the response of the hide beetle, *Dermestes maculatus*, to aggregation pheromone**. International Journal of Invertebrate Reproduction and Development 9**: 35-41.

Richardson, M. S., & Goff, M. L. (2001). Effects of temperature and intraspecific interaction on the development of *Dermestes maculatus* (Coleoptera: Dermestidae). **Journal of Medical Entomology 38**: 347-351.

Schroeder, H., H. Klotzbach, L. Oesterhelweg & K. Püschel. 2002. Larder beetles (Coleoptera, Dermestidae) as an accelerating factor for decomposition of a human corpse. **Forensic Science International 127**: 231-236.

Shean B. S., L. Messinger & M. Papworth. 1993. Observations of differential decomposition on sun exposed v. shaded pig carrion in coastal Washington State. **Journal of Forensic Sciences 38**: 938–949.

Smith, K.G.V. 1986. **A manual of forensic entomology**. Trustees of the British Museum, Natural History and Cornell University Press, London, United Kingdom. 205 p.

Tabor, K.L, C. C. Brewster & R.D. Fell. 2005. Insect fauna visiting carrion in southwest Virginia. **Forensic Science International 150**: 73-80.

Tabor, K.L., C.C. Brewster & R.D. Fell. 2004. Analysis of the successional patterns of insects on carrion in southwest Virginia. **Journal of Medical Entomology 41:** 785-795.

von Hoermann, C., J. Ruther & M. Ayasse. 2012. The attraction of virgin female hide beetles (*Dermestes maculatus*) to cadavers by a combination of decomposition odour and male sex pheromones. **Frontiers in Zoology 9**: 18.

von Hoermann, C., J. Ruther, S. Reibe, B. Madea & M. Ayasse. 2011. The importance of carcass volatiles as attractants for the hide beetle *Dermestes maculatus* (DeGeer). **Forensic Science International 212**: 173-179.

Watson, E. & C. Carlton. 2003. Spring succession of necrophilous insects on wildlife carcasses in Louisiana. **Journal of Medical Entomology 40:** 338-347.

Watson, E. & C. Carlton. 2005. Insect succession and decomposition of wildlife carcasses during winter and fall in Louisiana. **Journal of Medical Entomology 42:** 193-203.

Woodcock, L., D. Gennard & P. Eady. 2013. Egg laying preferences and larval performance in *Dermestes maculatus*. **Entomologia Experimentalis et Applicata 148**: 188-195.