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Role of Volatile Semiochemicals in the Host and Mate Location Behavior of *Mallodon dasystomus* (Coleoptera: Cerambycidae)

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Abstract Little is known of the role semiochemicals play in the mating systems of longhorned beetles (Coleoptera: Cerambycidae) in the primitive subfamily Prioninae. *Mallodon dasystomus* (Say), the hardwood stump borer, is a widely distributed prionine native to the southern US. Preferred hosts *of M. dasystomus* include oak, sweetgum, sugarberry and hackberry; although they also colonize a variety of other hardwoods. Here, we study the mate location behavior of *M. dasystomus* by testing the hypotheses that the sexes are mutually attracted to volatiles emanating from the larval host and that females release a volatile pheromone that is attractive to males alone. In a Y-tube olfactometer, male and female *M. dasystomus* responded to volatiles from host material (i.e., sweetgum and sugarberry). However, only males responded to females in the olfactometer, suggesting that females release a volatile sex pheromone. In choice experiments conducted in a greenhouse, we determined that both males and females prefer host over non-host material. In further bioassays in the greenhouse, males chose host material containing a live female over that containing a live male or host material alone. These findings are further evidence of the critical role host volatiles and pheromones play in mating systems of longhorned beetles.

Keywords Longhorned beetles · sex pheromone · kairomone · calling behavior

Introduction

The chemically-mediated host colonization and mating behavior of beetles in the family Cerambycidae, the longhorned beetles, has received little attention despite the economic importance and diversity of the group. The family includes more than

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35,000 described species (Lawrence 1982) and its members are among the most important pests of woody plants in natural and managed systems worldwide (see volumes indexed in Linsley and Chemsak 1997). Many attack domestic broadleaf trees and shrubs (Solomon 1995). The larvae are phytophagous, and colonize hosts that vary in quality ranging from healthy, moribund, and recently killed to even decomposing (Hanks 1999).

Male-produced sex or aggregation pheromones have been described for cerambycid species in the subfamilies Cerambycinae, Lamiinae and Spondylidinae/Aseminae (Lacey et al. 2004, 2007; Hanks et al. 2007; Silk et al. 2007; Millar et al. 2009; Ray et al. 2009, 2011; Fonseca et al. 2010; Pajares et al. 2010). In contrast, it appears that sex pheromones are produced by females in the subfamily Prioninae (Cervantes et al. 2006; Rodstein et al. 2009, 2011). The first volatile pheromone of this kind was isolated from *Prionus californicus* Motcholsky (Rodstein et al. 2009), and the compound was identified as (*3R, 5S*)-3, 5-dimethyldodecanoic acid (Rodstein et al. 2011). Female *P. californicus* also display a characteristic calling behavior while releasing pheromone—a female lowers her head and raises her abdomen while extending the ovipositor (Barbour et al. 2006). While calling, some females evert a membranous, cylindrical fluid-filled sac from their ovipositors and this structure is likely involved in the production and/or release of pheromone (Barbour et al. 2006). Male *P. californicus* also recognize females by a contact pheromone (Barbour et al. 2007); although the compounds that mediate mate recognition have yet to be identified. More recently, two methyl-branched hydrocarbons, 2Me-C_{26} and 2Me-C_{28}, were identified as the contact pheromone of another prionine, *Mallodon dasystomus* (Say) (Spikes et al. 2010). Female *M. dasystomus* display "calling" behaviors that are almost identical to those of *P. californicus* (Barbour et al. 2006), and similar to other beetles in which females produce volatile pheromones (e.g., Burkholder et al. 1974; Hammack and Burkholder 1981).

Host plant volatiles also play an important role in the reproductive biology of longhorned beetles. For some species, the sexes are united solely by their mutual attraction to volatiles emanating from the larval host or adult food plant (Hanks 1999). Additionally, many cerambycids are attracted to traps baited with host derived compounds like ethanol and turpentine (see review by Allison et al. 2004). *Monochamus galloprovincialis* Motschulsky (Lamiinae) is attracted to a blend of host compounds and *Ips* bark beetle pheromones (Pajares et al. 2004). Interestingly, these kairomones also synergize the activity of a male-produced aggregation pheromone, 2-undecyloxy-1-ethanol, in the field (Pajares et al. 2010). Host compounds may also be required for pheromones to be effective species-specific mate location signals. For example, male *Tetropium fuscum* (F.) (subfamily Spondylidinae/Aseminae; Monné and Hovore 2005; Bousquet et al. 2009), an exotic pest from Europe that has recently invaded Canada, and *T. cinnamopterum* Kirby, a beetle native to Canada, release the pheromone (*E*)-6,10-dimethyl-5,9-undecadien-2-ol (fuscumol), but host plant volatiles are required to elicit any behavioral response from conspecific females (Silk et al. 2007, 2010). Fuscumol also attracts *T. castaneum* when combined with a blend of host monoterpenes and ethanol (Sweeney et al. 2010). Moreover, the Asian longhorned beetle, *Anoplophora glabripennis* (Motchulsky), is more attracted to pheromone lures when they are combined with a mixture of host volatiles including (−)-linalool, (*Z*)-3-hexen-1-ol, linalool oxide, *trans*-caryophyllene, and *trans*-pinocarveol

(Nehme et al. 2010). For many species that attack weakened and moribund trees, volatile pheromones and host compounds may serve to expedite the location and subsequent colonization of these ephemeral resources. Nevertheless, the role of these semiochemicals in the mating system of cerambycids in the subfamily Prioninae, particularly those that attack hardwoods, remains poorly understood.

In this study, we use Y-tube olfactometry and bioassays performed in a greenhouse to test the hypotheses that the sexes of *M. dasystomus* can discriminate between host and non-host material and are mutually attracted to volatiles emanating from the larval host. We also test the hypothesis that females release a volatile sex pheromone that is attractive to males alone.

Materials and Methods

Natural History

Mallodon dasystomus, the hardwood stump borer, is a widely distributed prionine native to the southern United States. The elongate and robust adults are nocturnal, rather sedentary, vary in color from reddish brown to black and range in length from 23 to 47 mm (Solomon 1995). Females lay eggs near the base of stressed and dying trees at places where the wood is exposed, such as wounds or sites of previous infestation (Solomon 1995). *M. dasystomus* is one of the few prionines whose larvae feed on the boles of trees, while most species in this subfamily infest roots (Duffy 1953; Linsley 1959). Host preferences of *M. dasystomus* include sweetgum (*Liquidamber styraciflua*), sugarberry (*Celtis laevigata*), oak (*Quercus* spp.), hickory (*Caryae* spp.), willow (*Salix* spp.), boxelder (*Acer negundo*), and they are capable of infesting a variety of other hardwoods (Solomon 1995; Yanega 1996). Larvae typically complete their development in 3–4 years, and emerge as adults from May through July, leaving large ovoid emergence holes in the bark (Linsley 1962; Solomon 1995). In rare instances, adult specimens have been collected as early as April in south Florida and as late as October in northern locations (Thomas 1977; Solomon 1995; Yanega 1996). Natural enemies of *M. dasystomus* are chiefly larger woodpeckers, such as the pileated woodpecker, *Dryocopus pileatus* L., and the larvae are thought to be a major dietary component of the endangered ivory-billed woodpecker, *Campephilus principalis* L. (Tanner 1942; U.S. Fish and Wildlife Service 2011).

Y-Tube Olfactometer

We used a glass Y-tube olfactometer (6 cm OD, main tube 26 cm long, arm length 22 cm, 70° angle between the arms and a female ground glass joint (29/26) at each end) to measure the walking response of male and female *M. dasystomus* to conspecific adult beetles of each sex and volatiles emanating from host trees (i.e., sweetgum and sugarberry). Air was pulled through the system by a laboratory vacuum supply at a rate of ~1 L/min regulated by a high flow rotameter (Supelco, cat. no. 22550-U, Bellefonte, Pennsylvania), and air was purified with ~2 g of activated charcoal before entering the olfactometer. All bioassays were conducted during afternoons in the dark under a red light and ambient laboratory conditions. Odor sources were randomized

between the arms of the olfactometer to control for location effects, and the olfactometer was rinsed in acetone and air dried between trials. All beetles used in our experiments were reared from infested sweetgum and sugarberry at the USDA Forest Service Center for Bottomland Hardwoods Research (CBHR), Stoneville, MS. Mating status of beetles used in bioassays was unknown. Adult beetles used in bioassays were from 1 to 10 days old. Only vigorous active beetles were used in bioassays and were used no more than once per day.

To bioassay the response of adult beetles to a conspecific male or female in the olfactometer, an adult beetle (the odor source) was placed in a glass vacuum trap (trap bottle 60 mm OD × 300 mm overall length, 30 mm OD side and inner tubes, 55/50 joint, ChemGlass, cat. no. CG-4514-14, Vineland, New Jersey) which was connected to one arm of the olfactometer with ~15 cm of Tygon® tubing. An empty vacuum trap (control) was fitted to the other arm of the olfactometer. The position of the odor source chambers and associated tubing was switched between the arms of the olfactometer, and the olfactometer was rinsed in acetone and air dried between trials. The male or female that served as the odor source was replaced after every five trials and used only once per day. These assays were conducted at Purdue University, West Lafayette, IN from May 23, 2008 to June 10, 2008 and no more than 10 individuals were assayed per day. Adult beetles were shipped over-night on ice from the USDA Forest Service CBHR, Stoneville, MS (USDA–APHIS permit No. P526P-09-01631). In the laboratory, individual beetles were housed in cages of aluminum window screen (300 cm^3) with 9-cm glass Petri dishes covering top and bottom and provided a 10 % sucrose solution in a glass vial into which was inserted a cotton dental roll (Patterson Dental Supply, South Edina, Minnesota). Beetles were kept in an environmental chamber (Mod. No. 1-30BLL, Percival Scientific, Boone, Indiana) on a 16 L –29 °C:8D – 25 °C cycle that was 12 h out of phase with natural daylight, and maintained at 80 % humidity. Beetles were isolated in cages for at least 24 h before being used in bioassays. Bioassays were conducted 1 h after the onset of scotophase until the sixth hour of scotophase.

To measure the response of males and females to host volatiles in the olfactometer, ~3.0 g of bark and cambium were stripped from recently cut bolts of sweetgum and sugarberry (ends were sealed with paraffin wax) using a draw knife. The freshly cut bark and phloem was placed in a glass inner inlet adapter and connected to one arm of the olfactometer. An empty inlet adapter was connected to the other arm of the olfactometer to serve as a control. We assayed the response of females to both species of tree and males to sweetgum alone from June 19, 2010 to June 28, 2010 at USDA Forest Service CBHR. We then measured the response of males to sugarberry volatiles at Purdue University, West Lafayette, IN on July 8, 2010 under the same conditions as described above. For those assays performed at CBHR, adults were stored individually in a walk-in cooler (9 °C) upon emergence, and allowed to warm to room temperature in the dark before being used in bioassays.

A beetle was released at the downwind end of the main tube of the olfactometer and given 5 min to respond to an odor source by walking at least half way down (14 cm) one of the arms. Beetles that did not walk down either of the arms of the olfactometer within 5 min were recorded as “no response”. We tested the response of 20–43 adults to each odor source and, due to the sedentary nature of the beetles, first

compared the number of beetles that responded against our expectation of "no response" (i.e., beetles remaining in the main tube after 5 min) with a χ^2 goodness-of-fit test with a Yates' correction for continuity (StatSoft 2005). We then performed an additional χ^2 goodness-of-fit test (StatSoft 2005) to compare the number of responding beetles that choose the odor source with those choosing the clean air control.

Greenhouse

In an independent bioassay, we determined whether adult beetles could discriminate between host and non-host material by performing a choice-test bioassay in a greenhouse (20 m×15 m) at the USDA Forest Service CBHR. We tested whether males and females could discriminate between a group of five boles (~105×10 cm) of sweetgum and a group of bald cypress (*Taxodium distichum*); there is no record of *M. dasystomus* colonizing bald cypress. Logs in each group were placed upright and the groups were spaced 2 m apart centered along a line 5 m from one long wall of the greenhouse. For each trial, we released five beetles of the same sex positioned ~1.5 m apart along a line ~5 m downwind of treatments. Individuals were spaced apart along the release line to limit their interaction and to control for location effects. For each trial, beetles were allowed to respond to treatments for 1 h while we visually monitored their position. Beetles were considered to "respond" after climbing onto a bole within one of the treatments, after which they were removed. Beetles that did not climb onto a bole within an hour were recorded as "no response". The response of males and females to the treatments was tested separately from 21:00 to 03:00 h on June 21–23, 2011; skies clear, air temperatures ~30 °C. After each trial, we switched positions of the treatments so that each treatment occupied all positions at least once per night. The response of males and females to the odor sources were tested on separate nights. All beetles used in the bioassays were reared from infested material and only those that were active and apparently healthy were used. Adults were stored individually in a walk-in cooler (9 °C), and allowed to warm to room temperature in the dark before being used in bioassays. Individuals were only used once per night and for a maximum of four nights. Adult beetles that served as part of the treatment were used once. We compared the response of both 28 males and 28 females to sweetgum or bald cypress with a χ^2 goodness-of-fit test (StatSoft 2005)

In the greenhouse, we also tested for the presence of attractant pheromones by performing choice-test bioassay. Three sets of five equally-sized boles (~85× 14 cm) of freshly cut host logs (four sugarberry and one sweetgum) were placed upright 2 m apart and 5 m away from one long wall of the greenhouse. One set of boles contained a single male *M. dasystomus,* a second contained one adult female, and the third set was comprised of host logs alone. Four or five males or females were released 5 m downwind of the treatments and allowed 1 h to respond (see description of response above). Three trials for each sex were performed each night under red light between 21:00 and 03:00 h from June 15 to June 20, 2011; skies clear, air temperatures ~30 °C. We compared the response of 77 adults to logs that contained either a male or female or logs alone with a χ^2 goodness-of-fit test (StatSoft 2005).

Results and Discussion

Adult males alone showed a significant response to females in the olfactometer (Table 1). Of the responding males, 76.9 % chose the female over the clean air control (see Table 1). However, 80 % of females tested displayed "no response" to the other females and remained in the main tube of the olfactometer (Table 1), suggesting that females are not attracted to other females by semiochemicals. Moreover, neither males nor females responded significantly to males in the olfactometer (see Table 1), illustrating the sedentary nature of these beetles in the absence of a stimulus. In the greenhouse, males responded significantly to the treatment containing a female; 24 responded to the female treatment, 10 to the male treatment and 6 to the control (6 no response; totals significantly different $\chi^2_{2,\ 40} = 13.4$, $P = 0.0012$). However, females displayed no preference for any of the treatments; 11 responded to the female treatment, 15 to the male treatment and 6 to the control (3 no response; $\chi^2_{2,40} = 0.62$). The preference of male *M. dasystomus* for live females in the olfactometer and greenhouse provides evidence that females produce an attractant sex pheromone.

Male and female *M. dasystomus* were significantly attracted to volatiles of cut sweetgum and sugarberry in the y-tube olfactometer (see Table 1). In the greenhouse adults responded significantly to sweetgum, with 28 of 30 beetles of each sex choosing sweetgum over bald cypress ($\chi^2_{1,30} = 13.87$, $P < 0.001$). These results support the hypothesis that the sexes are mutually attracted to volatiles emanating from the larval host. Both sexes show no preference for cypress, which is not a documented host. Although *Prionus pocularis* Dalm. is attracted to stressed Virginia pines (Hines and Heikkenen 1977), this is the first demonstration that the sexes of a cerambycid belonging to the subfamily Prioninae are attracted to odors of a hardwood host plant. Other cerambycids from various subfamilies that feed on hardwood hosts show a similar attraction to host volatiles. Within the subfamily Cerambycinae, for example, *Xylotrechus colonus* F., *Megacyllene caryae* (Gahan) and *Neoclytus mucronatus mucronatus* (F.) respond to hickory volatiles (Ginzel and Hanks 2005) and female and male *Hoplocerambyx spinicornis* Newman locate newly felled host trees by plant volatiles (Singh and Misra 1981). Both sexes of *Phoracantha semipunctata* (F.) congregate on stressed or felled eucalyptus trees and are attracted

Table 1 Number of male and female *M. dasystomus* responding to the indicated odor source and the choice of the responding beetles (see Materials and Methods)

Sex	Odor source	*N*	# responding	χ^2 statistic (*P*)	# choosing odor source	# choosing control	χ^2 statistic (*P*)
Male	Female	40	26	35.6 ($P<0.001$)	20	6	4.06 ($P<0.05$)
	Male	21	2	0.52 ($P=0.47$)			
	Sweetgum	36	30	48.1 ($P<0.001$)	23	7	4.59 ($P<0.05$)
	Sugarberry	43	28	38.6 ($P<0.001$)	26	2	12.6 ($P<0.001$)
Female	Female	20	4	2.5 ($P=0.11$)			
	Male	23	3	1.43 ($P=0.23$)			
	Sweetgum	37	31	49.9 ($P<0.001$)	23	8	3.86 ($P<0.05$)
	Sugarberry	41	32	49.3 ($P<0.001$)	25	7	5.49 ($P<0.05$)

to volatiles emitted from eucalyptus bark (Hanks et al. 1996). Moreover, *Plagithmysus bilineatus* Sharp adults are more attracted to stressed ohia trees than healthy trees (Stein and Nagata 1986).

In contrast to the male-produced aggregation pheromones of the cerambycines, it appears that female *M. dasystomus* produce and emit the attractant pheromone. In fact, the use of female-produced attractants may be widespread throughout the family Cerambycidae, particularly in the subfamily Prioninae. For example, traps baited with a blend of stereoisomeres of synthetic 3,5-dimethyldodecanoic acid, the female produced sex pheromone of *Prionus californicus,* captured males of seven other *Prionus* species (Barbour et al. 2011). Moreover, the prionines *Prionoplus reticularis* White, *Prionus laticollis* (Drury), and *Prionus emarginatus* Say display behaviors consistent with pheromone use (Edwards 1961; Benham and Farrar 1976; Gwynne and Hostetler 1978). More recently, other females within the subfamily Prioninae (Cervantes et al. 2006; Barbour et al. 2006) and even those in the subfamily Lepturinae (pers. obs.) have been reported to demonstrate calling behaviors associated with the release of pheromone.

Stressed and dying host trees, like those colonized by *M. dasystomus*, become sporadically available when they are weakened by environmental stresses (reviewed by Hanks 1999) or abiotic factors such as mechanical damage or wounding. The suitability of these hosts to developing larvae declines rapidly as subcortical tissues are degraded by various xylophagous competitors–including buprestid and scolytid beetles and other cerambycid species. For those species that mate on stressed larval host plants, their ability to rapidly locate an appropriate host directly influences their reproductive potential (Goldsmith et al. 1996). Interestingly, the digestive tracts of both sexes of *M. dasystomus* are atrophied (pers. obs.), suggesting that they do not feed as adults and are also short lived (2–3 weeks; MAP pers. obs.). Consequently, selection favors behaviors in these adults that expedite rapid mating and oviposition, and early colonizers of moribund trees are afforded better larval nutrition (Ginzel and Hanks 2005). A mutual response of females and males to larval host-derived volatiles and the reliance on sex pheromones to unite sexes may be adaptive because it not only expedites mate location, but also subsequent colonization of the host (see Landolt and Phillips 1997). Similar to the Cerambycinae, other species of the Prioninae that require stressed hosts may show similar reproductive behaviors. The use of host kairomones for mate location may be more widespread within the subfamily, but has yet to be explored for any of the more typical root-feeding species.

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