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The Role of Olfactory Cues in Short-Range Mate Finding by the Emerald Ash Borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)

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Abstract We investigated the relative importance of olfaction versus vision in the mate-finding behavior of *Agrilus planipennis*. When coupled in male–female, male–male and female–female pairs, attempts to mate occurred only in the male–female pairs, suggesting that beetles can identify the opposite sex before attempting to mate. In a set of sensory deprivation experiments with male–female pairs, we evaluated whether males could find females when deprived of their sense of olfaction, vision or both. Males whose antennae were blocked with model paint took significantly longer to find females and spent less time in copula compared to untreated males. Males whose eyes were similarly blocked did not differ in their mate finding capacity compared to untreated males. In a third experiment that compared both olfaction and vision, olfactorily impaired beetles never mated whereas the mate finding potential of visually impaired beetles did not differ from that of untreated beetles. Our results indicate that males can identify females before coming into physical contact with them, and that at short range (≤5 cm), volatile cues detected by olfaction are involved in mate finding by *A. planipennis*.

Keywords Sex discrimination · sensory deprivation · olfaction · vision · mounting · short-range sex pheromone

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Introduction

Mate location in insects can be mediated via visual (Gorb 1998; Szentesi et al. 2002), olfactory (Ginzel and Hanks 2003; Lopes et al. 2005; Johansson and Jones 2007), vibrational/acoustic (Bailey 2003; Cocroft and Rodriguez 2005) or tactile cues (Thornhill and Alcock 1983). In temperate climates, where the mating season is short, insects must recognize mature conspecifics of the opposite sex efficiently; thus they may use multiple cues to find and choose their mates (Candolin 2003). Before coming into physical contact with each other, insects can use visual cues to orient towards potential mates, or employ long or short range olfactory cues to find them. These olfactory cues emitted by either males or females are usually volatile compounds (long or short range sex pheromones) (Cardé and Minks 1997) or contact pheromones (cuticular hydrocarbons) (Blomquist et al. 1996; Ginzel and Hanks 2003; Ginzel et al. 2003; Howard and Blomquist 2005) that are species specific and can indicate the sexual maturity of the insect.

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is an invasive pest native to China, Japan and Korea (Wei et al. 2004), that is causing widespread mortality of ash trees, *Fraxinus* spp. in the Midwestern United States of America (Haack et al. 2002; Poland and McCullough 2006) and southern Ontario in Canada. In mid-June, adult beetles emerge from ash trunks and branches and feed on leaf margins for about 2 weeks as they mature. When beetles reach maturity in July, they land and crawl on bark crevices where they mate and lay eggs (Bauer et al. 2004). Tree mortality occurs in outbreaks, when extensive larval feeding on phloem and cambium of branches and tree trunks disrupts translocation of water and nutrients to the crown (Poland and McCullough 2006). Studies on the biology and behavior of *A. planipennis* are limited because it is a recent pest in North America and there are no recorded outbreaks on native hosts in Asia. Most current investigations are from a management perspective, in an attempt to develop potent attractants and repellents to trap, monitor and control the beetle.

An adequate understanding of the ecology and behavior of an insect pest is required before management tactics can be successfully employed to control populations in the field. We investigated the mating behavior of *A. planipennis* to determine the relative importance of olfaction and vision when beetles locate their mates. The dorsal surface of the elytra of both sexes of *A. planipennis* is bright emerald in color, and females are larger on average than males (McCullough and Roberts 2002; Lyons and Jones 2005). When the elytra are lifted, a majenta abdomen is revealed. During mating, males hover over the tree bark, swoop down and land on females that are resting or crawling in bark crevices or on leaves and then mount them (Lelito et al. 2007; Rodriguez-Saona et al. 2008; Pureswaran, pers. obs.). It is therefore possible that either vision, olfaction or both are used by males to locate females.

To identify the sensory cues involved in mate location we conducted a series of experiments in the laboratory that involved (1) a test of sex discrimination and (2) sensory deprivation tests, in which, after depriving males and/or females of their sense of olfaction and vision, we measured (a) the time they took to find their mates in closed arenas and (b) the time they spent in copula once they found each other.

Materials and Methods

Collection and Treatment of Beetles

Green ash, *Fraxinus pennsylvanica* Marsh, infested with *A. planipennis* were collected near Brighton and Lansing, MI. Trees were felled and bucked into 90-cm-long bolts and stored at 4°C. As beetles were required for experiments, they were allowed to complete development at 25°C and emerge in cardboard rearing tubes. They were separated by sex and kept in 295 ml plastic beverage containers with a leaf of evergreen ash, *F. uhdei* (Wenzig) Linglesh as food in a vial of water. Containers were stored in growth chambers at 25°C, >70% relative humidity, and a 16:8 L:D photoperiod. Beetles were provided with fresh food twice a week, for 2 weeks, until they were sufficiently old (15–20 days) for use in experiments.

Test of Sex Discrimination

To determine whether beetles could discriminate between males and females, we tested whether beetles attempted to mount beetles of the same sex when they were mature. Aged virgin beetles were separated into male–male, male–female and female–female pairs that were placed in a container as described above. Beetles were observed every 20 min for a 5-h period for attempts to mount their partner. The proportion of beetle pairs that attempted to mount was recorded. We had a sample size of 10 replicates per treatment. The experiment was set up in randomized complete blocks on a laboratory work bench. All experiments were conducted at 25–28°C and 70% relative humidity, between 1000–1700 h EDT, which is the time of most sexual activity by the beetles (Rodriguez-Saona et al. 2008; Pureswaran pers. obs.).

Sensory Deprivation Experiments

We conducted a set of three experiments where beetles were deprived of their sense of smell or sight by blocking their antennae or eyes respectively, with red model paint (#1150 flat red rouge mat) (The Testor Corp., Rockford, IL). Beetles were placed together in male–female pairs in a beverage container as described above. We used a triple 0 artist's brush to carefully apply paint on the antennae or eyes while viewing beetles through a dissection microscope. For all experiments, untreated beetles were used as positive controls, and beetles with a similar quantity of paint on each wing as was applied to the eyes and antennae, were used as painted controls. The goal of using painted controls was to detect if the paint was lethal to the beetles or whether odors from the paint disrupted mating behavior altogether. If a beetle died during the experiment, the pair was excluded from the analysis.

Beetles were treated as follows: (1) Painted antennae experiment ($n=15$): (i) untreated male and untreated female (ii) both male and female with paint on wings (iii) untreated male and female with painted antennae (iv) male with painted antennae and untreated female and (v) both male and female with painted antennae; (2) Painted eyes experiment (n=22):(i) untreated male and untreated female (ii) both male and female with paint on wings (iii) untreated male and female with painted

eyes (iv) male with painted eyes and untreated female and (v) both male and female with painted eyes; (3) Painted antennae and eyes experiment (n=10): In this experiment, we compared the effects on mating attempts of impairing olfaction, vision, and both senses in both sexes. Treatments were: (i) untreated male and untreated female (ii) both male and female with painted wings (iii) both male and female with painted eyes (iv) both male and female with painted antennae and (v) both male and female with painted antennae and eyes.

Beetles were observed every 20 min for a 5-h period for attempts to mount their partners. The proportion of beetle pairs that attempted to mount was recorded. The amount of time beetles took to find each other and the time spent in copula were noted. If either the male or female died before attempting to mate, the pair was excluded from the experiment. The experiment was set up in randomized complete blocks on a laboratory work bench. When no mounting occurred within the time frame of the experiment (300 min), a conservative value of 320 min was assigned, with the assumption that given enough time in the confined area, the male would eventually find the female.

Statistical Analyses

In all experiments, to test whether the proportion of beetles that successfully mounted and mated differed significantly from the proportion that did not mount, we used a chi square test for proportions (PROC FREQ). In sensory deprivation experiments, to test (1) whether the time males took to find females and (2) the time spent in copula differed significantly among treatments, we analysed the $\log_{10}(x+1)$ transformed data using multivariate analysis of variance (PROC GLM) with treatment and block as sources of variation, followed by the Ryan-Einot-Gabriel-Welsch multiple comparisons procedure.

Treatments were then weighted by the extent to which beetles were experimentally manipulated (weighting the treatments in the statistical analysis represented the extent to which the beetles' senses were impaired, i.e. untreated beetles being the least impaired, and both sexes with painted antennae being the most impaired in the painted antennae experiment) and further analyzed by proportional hazards regression analysis (PROC PHREG) (Allison 1995) to determine the percent decrease in mating success [(1-hazard ratio)*100] due to our treatments. If mounting did not occur by 300 min, the observations were right censored. We modeled time to mounting by the censored variable, using treatment and block as independent variables. The EXACT option was used for handling ties. All analyses were performed using SAS Institute Inc. version 9.1 (2002–2003) statistical software, and α=0.05.

Results

Test of Sex Discrimination

Mounting and subsequent mating were successful 90% of the time by male–female pairs ($\chi^2_{0.05,2}$=21.8, P<0.0001) (Fig. 1). No attempts to mount were made by male–

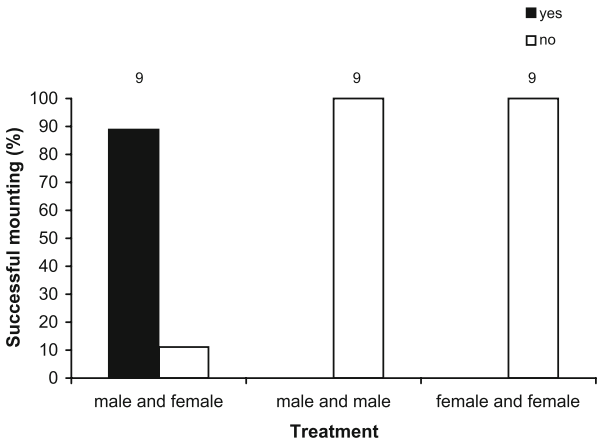

Fig. 1 Percent successful mountings among opposite sex and same sex pairs in the sex discrimination experiment. Sample sizes (*n*) for each treatment are shown above bars.

male or female–female pairs (Fig. 1). Beetles in same sex combinations did not approach each other in the arena.

Sensory Deprivation Experiments

There was no significant effect of block in any of the three experiments ($P>0.05$), indicating that there was no environmental gradient that influenced mating success of beetles in our experiments.

Painted Antennae Experiment When we impaired the sense of olfaction to various degrees, there were significant effects of treatment, on the time males took to mount females and remain in copula (MANOVA Wilk's $\lambda=0.66$, $F_{8,\ 130}=3.8$, $P=0.0005$; time to mounting: $F_{4,\ 66}=4.7$, $P=0.002$; time spent in copula $F_{4,\ 66}=6.7$, $P=0.0001$ (Fig. 2, Table 1). Eighty percent of untreated pairs mounted and mated successfully, and the proportion of successful mountings declined as our treatments became more invasive to the beetles (i.e. the extent of experimental manipulation increased) ($\chi^2_{0.05,4}=21$, $P=0.0003$) (Fig. 2a). Untreated beetles took the shortest time to initiate mounting and remained in copula longer than beetles in any other treatment (Fig. 2a,b). Beetles with painted wings did not differ significantly from untreated beetles, indicating that painting the beetles was not lethal and did not interfere with their mate finding abilities. When untreated males were paired with females whose antennae were painted, there was no difference in the time to mounting or in the time spent in copula compared to untreated controls (Fig. 2b,c). However, in the treatments where male antennae were painted, beetles took significantly longer to initiate mounting and spent less time in copula compared to treatments where males were untreated (Fig. 2b,c). Painting the antennae of females did not appear to affect mounting success. There was a significant drop of 42% in mating success as we increasingly disrupted the olfactory capabilities of the beetles (Table 1).

Painted Eyes Experiment When the vision of males, females or both sexes was blocked, there was no significant difference in the proportion of successful mating

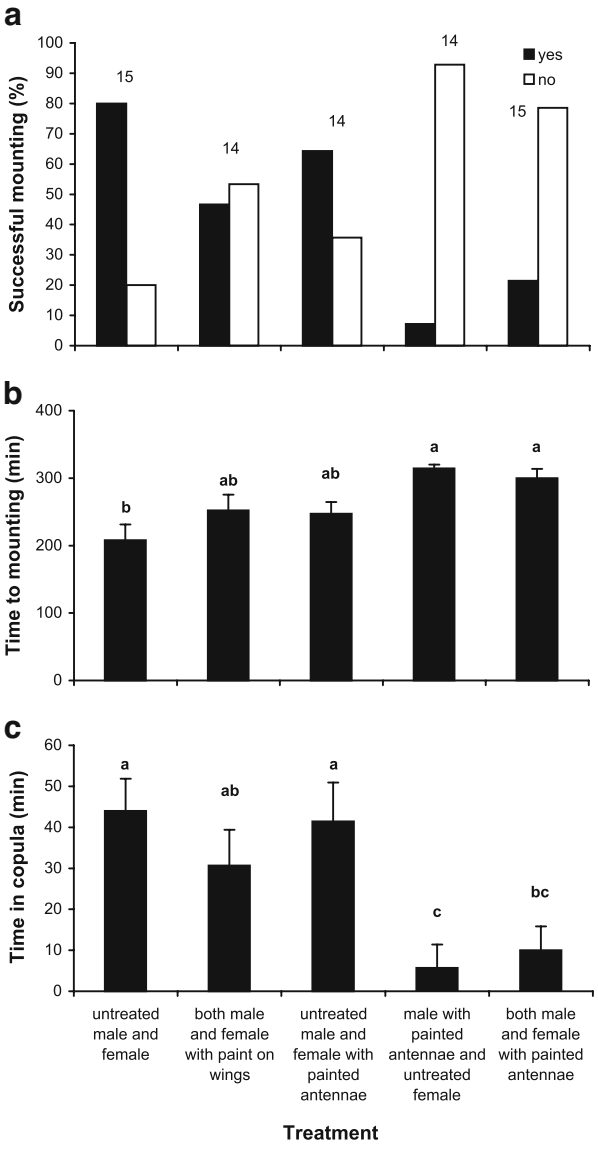

Fig. 2 Percent successful mountings among treatments in descending order of olfactory impairment (**a**) in the painted antennae experiment. Average time taken for beetles to find their mates and initiate mounting (**b**) and time spent in copula (**c**). *Bars with the same letter* are not significantly different, REGW-multiple comparisons test, $P<0.05$. Sample sizes (n) for each treatment are shown *above first set of bars*.

pairs compared to mating by the untreated controls ($\chi^2_{0.05,4}=8.4$, $P=0.08$) (Fig. 3a). There were also no significant differences in the time beetles took to initiate mounting or remain in copula (MANOVA Wilk's $\lambda=0.92$, $F_{8,198}=1.04$, $P=0.4$; time to mounting: $F_{4,100}=0.94$, $P=0.44$; time spent in copula: $F_{4,100}=1.8$, $P=0.13$) (Fig. 3b,c). The decrease in mating success of 17% with increasing disruption of vision from one treatment to the next, was not statistically significant (Table 1).

Painted Antennae and Eyes Experiment There was no difference in the proportion of successful matings between untreated and painted controls. However, while 20% of

Table 1 Results of Proportional Hazards Regression Analysis

Experiment	Chi-square	*P* value	Hazard ratio	Decrease in mating success from one treatment to the next (%) with increasing impairment of olfaction or vision
Painted antennae	15.1	0.0001	0.58	42
Painted eyes	2.8	0.09	0.83	17
Painted antennae and eyes	10.1	0.002	0.39	61

Treatments for each experiment in descending order of experimental manipulation are on x-axis labels of Figs. 2, 3, 4. Treatments represent the extent to which the beetles' senses were impaired, i.e. untreated beetles being the least impaired, and both sexes with painted antennae being the most impaired in the painted antennae experiment

the beetles whose eyes were painted mated successfully, no attempts to mount were observed in beetles whose antennae alone were painted, or both antennae and eyes were painted ($\chi^2_{0.05,4}=13.8$, $P=0.008$) (Fig. 4a). There was no difference in the time beetles took to initiate mounting or remained in copula among untreated beetles, beetles with painted wings and painted eyes, although beetles with painted eyes did not differ significantly from those whose antennae were painted (Fig. 4b,c). Untreated controls were more successful at mating than beetles that were olfactorily impaired by painting their antennae (MANOVA Wilk's $\lambda=0.66$, $F_{8,\ 80}=2.27$, $P=0.03$; time to mounting: $F_{4,\ 41}=4.2$, $P=0.006$; time spent in copula: $F_{4,\ 41}=4.1$, $P=0.007$). There was a 61% decrease in mating success with increasing impairment (Table 1).

Discussion

In general, male insects actively search for females, while females are more sedentary and often emit or display cues with which males can locate them (Thornhill and Alcock, 1983). We present evidence that at short range (≤5 cm), male *A. planipennis* can locate females before coming into physical contact with the other beetle in the mating arena. In the sex discrimination experiment, same sex pairs did not initiate mounting (Fig. 1) and appeared to avoid each other in the arena while heterosexual pairs readily mounted each other and mated, indicating that beetles could discern the sex of the other individual in the arena before attempting to copulate.

Beetle pairs in which male antennae were blocked with paint and paired with untreated females had fewer successful mountings, took longer to find their mates, and remained in copula for shorter duration than beetle pairs in which the male was untreated, but the female's antennae were blocked with paint (Fig. 2a,b,c). It appears that males initiate mounting and use short range volatile chemical cues produced by females to identify and locate suitable partners. Chemical cues are usually good indicators of an individual's reproductive state as physiological changes associated with maturity are often manifested by changes in body chemistry (Thornhill and Alcock 1983).

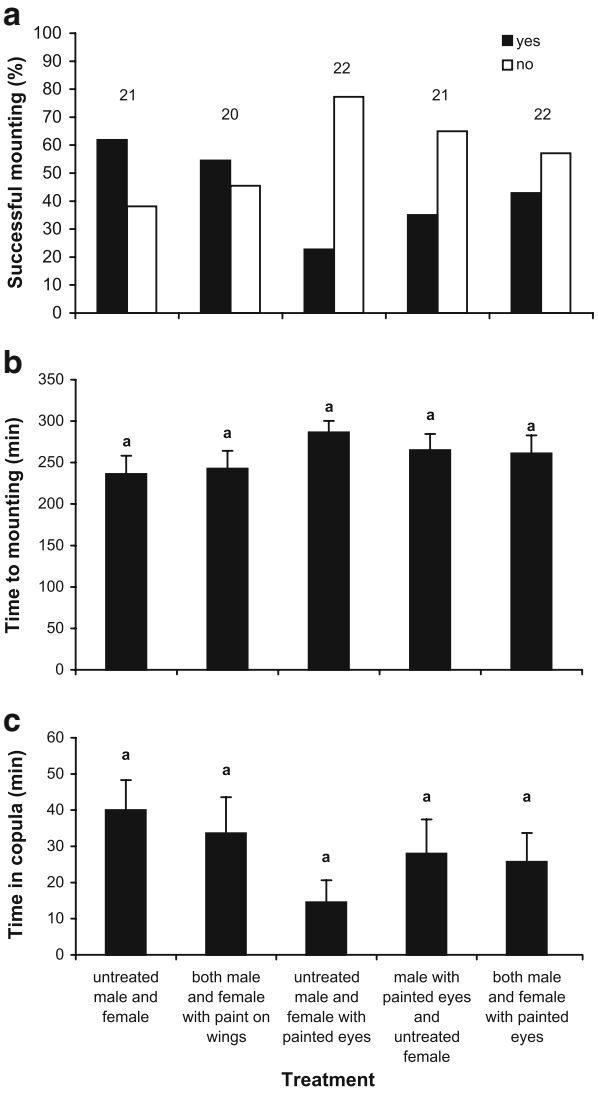

Fig. 3 Percent successful mountings among treatments in descending order of visual impairment (**a**) in the painted eyes experiment. Average time taken for beetles to find their mates and initiate mounting (**b**) and time spent in copula (**c**). *Bars with the same letter* are not significantly different, REGW-multiple comparisons test, $P<0.05$. Sample sizes (n) for each treatment are shown *above first set of bars*.

Sex pheromones are used in many species of insects for mate recognition and assessment (Johansson and Jones 2007). In insects in particular, there are benefits of chemical communication for mate location because of lower relative costs compared to energetically costly mechanisms like producing vibrations/acoustic cues (Alcock 1989; Candolin 2003). The use of non-contact signals in the mating behavior of *Agrilus* spp. is unknown. In the two-lined chestnut borer, *A. bilineatus* (Weber), more males landed on cages containing females compared to empty cages (Dunn and Potter 1988), suggesting that females may release sex pheromones.

In a study on the behavior of *A. planipennis*, Rodriguez-Saona et al. 2008, found that males seemed to actively search for mates on tree trunks, and often oriented towards and landed on other beetles of both sexes. Males hover over tree trunks and

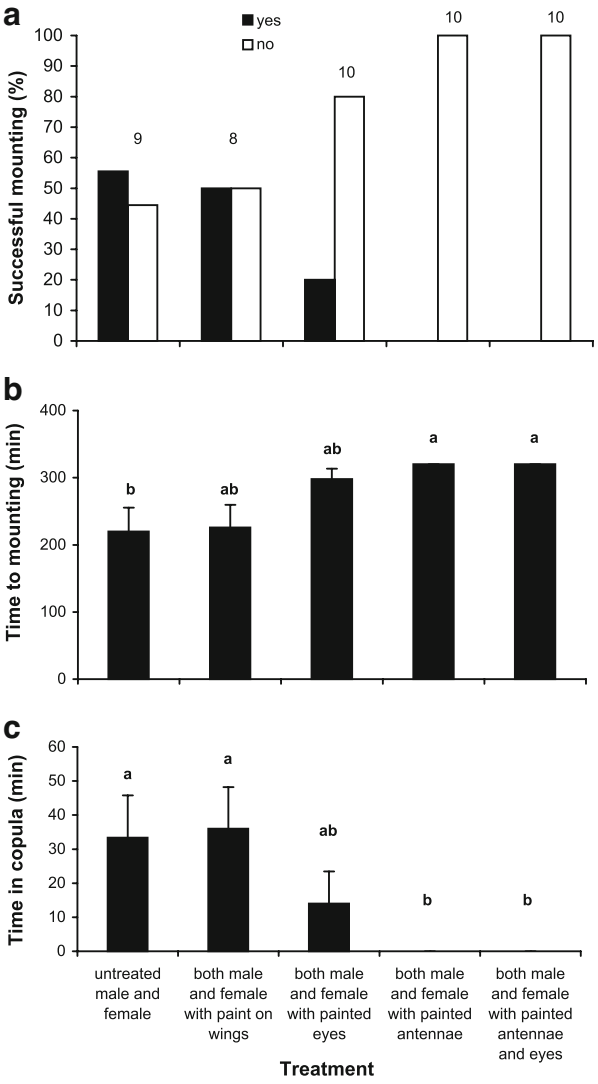

Fig. 4 Percent successful mountings among treatments in descending order of olfactory and visual impairment (**a**) in the painted antennae and eyes experiment. Average time taken for beetles to find their mates and initiate mounting (**b**) and time spent in copula (**c**). *Bars with the same letter* are not significantly different, REGW-multiple comparisons test, $P<0.05$. Sample sizes (n) for each treatment are shown *above first set of bars*.

around foliage to find females that are larger and sedentary, sitting on leaves or trunks awaiting males (Lelito et al. 2007; Rodriguez-Saona et al. 2008). Other males were generally ignored and not pursued for copulation even if males landed on them, suggesting that a visual component may be involved in orienting towards conspecific females at long range (Lelito et al. 2007; Rodriguez-Saona et al. 2008). Encounters with females were followed by mating attempts where the male positioned his legs to grip the female and initiated copulation. However, no courtship rituals by males or corresponding displays by females were observed by Rodriguez-Saona et al. (2008) or in our study, even though our arenas were fairly small (295 ml container), that would suggest the involvement of a strong short range visual component in mate finding.

In a study of long range mating behavior in the field, Lelito et al. (2007) report that when washed and unwashed dead males and females were pinned on trees, male beetles that were seeking mates could not differentiate among treatments, and suggest that males might visually identify conspecifics at long range (30–100 cm) and land on them. After landing, they recorded that more time was spent on unwashed females, indicating that contact cues may be involved in mate recognition after landing. In our experiments, male beetles whose vision was impaired fared just as well as untreated beetles in their mate finding abilities (Figs. 3, 4), indicating that visual cues are less important than olfactory cues at short range (≤5 cm) in the mating behavior of *A. planipennis*. When mating occurred, mounting by the male was usually quick and vigorous, with copulation lasting about 60 min.

In a similar study on mate location by a longicorn beetle, *Glenea cantor* (Fabr.) (Coleoptera: Cerambycidae), Lu et al. (2007) demonstrated the absence of long range olfactory cues in mate location. In this case long-range attraction of both sexes to weakened host trees brought them together and did not require the use of long-range sex pheromones. However, by removing terminal antennal segments in males and/or blocking their vision with paint, they showed that vision and a female sex pheromone function in mate location by males, at a short range of 3–3.5 cm or during contact, respectively.

We propose the existence of a putative sex pheromone that mediates the mating behavior of *A. planipennis*, and suggest that it operates before beetles come into physical contact with each other, at a short range (<5 cm). Unlike many tree-killing scolytids that use long-range aggregation pheromones (Wood 1982; Raffa et al. 1993) which also function in mate finding, the survival of *A. planipennis* on the trees that it infests is not contingent on the tree's death. It appears that both sexes of *A. planipennis* can locate susceptible ash trees using a combination of visual and volatile cues that emanate from them (Rodriguez-Saona et al. 2006; Pureswaran et al. unpublished data), and do not necessarily have to form aggregations on trees to survive and reproduce. In the red milkweed beetle, *Tetraopes tetrophthalmus* (Forster) (Coleoptera: Cerambycidae), Reagel et al. (2002) found no evidence for mate location by long-range pheromones or vision. Mate location appeared to be facilitated by attraction and accumulation of both sexes on host plants.

Long-range attraction to host plants by both sexes appears to preclude the need for long range sex pheromones. Short-range sex pheromones, while indicating the sex and maturity of the individual may be complex. They may possess multiple components, vary quantitatively among individuals, and may be produced only during a very short period in an individual's life time (Johansson and Jones 2007), making their isolation and identification challenging. Bartelt et al. (2007) identified a macrocylic lactone, (3Z)-dodecen-12-olide from the volatile emissions of female *A. planipennis* that was sensed by the antennae of both sexes. However, no behavioral activity for this compound has been reported. Although there are behavioral indications that mate finding is chemically mediated, no sex pheromone of any kind (long/short range or contact) has been chemically identified to date for *A. planipennis*. A systematic analysis of the volatile profiles of *A. planipennis* at different stages of its life history is required to identify and isolate volatile cues involved in mate recognition.

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