

Adults of the cerambycid beetle *Megacyllene caryae* use both olfactory and visual information to locate mates

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Abstract

Many species of beetles in the family Cerambycidae use volatile pheromones to facilitate the location of mates. Visual cues may also influence the location of mates, as the adults of many species of cerambycids are often brightly patterned and diurnal. Theory predicts that combining signals or cues of different modalities (e.g., chemical, visual) to transmit information will increase the likelihood of an organism responding to this information, compared to when the signal or cue is presented alone. Here, we test the hypothesis that attraction of adults of the cerambycid beetle *Megacyllene caryae* (Gahan) (Coleoptera: Cerambycidae, Clytini) to their pheromones will be increased when visual cues are present. Consistent with that hypothesis, the number of beetles caught by traps baited with pheromones was increased 3.4-fold when a dead adult beetle of that species was attached to the trap, relative to those with just pheromone alone. Capture of *M. caryae* in our study was also influenced by the position of traps within forest stands, with traps at 100 m within stands catching 2.5× as many beetles as traps at the forest edge. These findings suggest that vision and visual cues play an important role in the location of mates by cerambycid beetles and warrant further research. Also, the inclusion of visual cues on traps may enhance the efficacy of trapping cerambycid beetles, such as the detection of species that are non-native and potentially invasive, or when monitoring species that are native and of conservation concern.

Introduction

Rapid location of mates is critical for animals that utilize habitats that are ephemeral in space or time (Shorrocks, 1990; Ginzl & Hanks, 2005). Many species of beetles (Coleoptera) in the family Cerambycidae prefer to lay their eggs on trees that are stressed, weakened, or recently killed (Hanks & Wang, 2017). There is intense competition for these resources, as they are distributed as discrete patches and the suitability of trees for colonization by organisms that live within wood can change quickly (Ulyshen, 2016).

To facilitate the discovery of mates, many cerambycid species use chemical signals (i.e., pheromones) that volatilize over long ranges (Millar & Hanks, 2017). Response to signals produced by potential mates often can be enhanced by the use of information from more than one modality (e.g., chemical or visual) (Candolin, 2003; Hebets & Papaj,

2005). The adults of many cerambycid species have bright patterns on their bodies and are diurnal (i.e., active during the day; Linsley, 1959). This suggests that visual information may also act as a reliable cue for the location of mates by cerambycids at long ranges (Endler, 1992).

The type of visual information that can influence the location of mates by insects includes – but is not limited to – or size of a potential mate, as well as stereotypical movements that may act to signal the identity and/or quality of the insect that is performing the behavior (Thornhill & Alcock, 1983). At short ranges, beetles in the family Cerambycidae respond to visual information such as the color (Wang, 2002) and the shape and size of models and conspecifics (Fukaya et al., 2004, 2005). It is unknown whether visual information is important to the location of mates by cerambycids at distances greater than a few centimeters, and whether visual information interacts with information from other modalities (e.g., chemical) to enhance attraction, thus allowing beetles to rapidly mate and colonize trees.

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The cerambycid *Megacyllene caryae* (Gahan), commonly known as the hickory borer, is a yellow and black patterned beetle that visually and chemically mimics wasps in the family Vespidae (Mitchell et al., 2017). Larvae of *M. caryae* develop in hickories that are dying or recently dead, and the adults aggregate and mate on trees that have fallen, as well as firewood that has been cut recently (Linsley, 1964; Ginzel & Hanks, 2005). Upon the location of a tree that is suitable for colonization by the larvae of *M. caryae*, adult males emit an aggregation-sex pheromone (sensu Cardé, 2014) that consists of (2*S*,3*R*)- and (2*R*,3*S*)-2,3-hexanediol, (*S*)-(-)-limonene, 2-phenylethanol, (-)- α -terpineol, nerol, and citral, an isomeric blend of neral and geranial (Lacey et al., 2008). Citral is a major component (i.e., attractive when presented alone) of the aggregation-sex pheromone blend of *M. caryae* and adults of both sexes of *M. caryae* are strongly attracted to traps baited with citral (e.g., Lacey et al., 2008; Millar & Hanks, 2017).

In this study, we tested the hypothesis that orientation of *M. caryae* to a major component of its aggregation-sex pheromone on potential host trees will be enhanced by visual information associated with conspecifics. Our results contribute to a better understanding of the sensory ecology of *M. caryae*, as well as provide insights into the development of traps that increase the likelihood of detecting species that are rare such as those that are of conservation concern, or recent introductions of exotic species that may be invasive.

Materials and methods

Study site and trees

Field bioassays were conducted at the Vermillion River Observatory (40.0655, -87.561), a 192-ha second growth eastern deciduous forest owned by the University of Illinois. In our experiment, we used 90 shagbark hickories [*Carya ovata* (Mill.) K. Koch (Juglandaceae)] that appeared undamaged and healthy, and that were at least 10 m apart. Distance of each tree from the nearest forest edge was estimated using Google Earth (<https://www.google.com/earth>) from its GPS position.

Experimental design

On each tree we attached two traps of different designs that operated as a unit (Figure 1): (1) sticky traps were transparent plastic sheets coated with an adhesive (clear adhesive roll trap; 15 × 15 cm; Alpha Scents, West Linn, OR, USA), and (2) bucket traps, constructed from acetate copier transparency sheets (Staples, Framingham, MA, USA) that were attached to a 946-ml plastic container (WNA Plastics, Chattanooga, TN, USA). The sticky traps were stapled to tree trunks at 2.5 m above the ground, and

bucket traps were attached just below the sticky traps so as to capture insects that had escaped. Interior surfaces of bucket traps were coated with fluoropolymer dispersion Fluon (Northern Specialty Chemicals, Dudley, MA, USA) to render the surface slippery and prevent insects from escaping. Preliminary research revealed that some insects were capable of escaping from sticky traps, thus necessitating the addition of the bucket traps.

We used the bodies of air-dried, dead adult *M. caryae* as visual cues in our study. Beetles had been previously trapped during field assays in 2014 and stored in 70% ethanol. Solid-phase microextraction (SPME; 65 μ m PDMS/DVB Fused Silica fiber, Supelco 57310-U 50-300MW) was used to confirm that no volatile chemicals associated with *M. caryae* emanated from the dead beetles used as visual cues, and that ethanol used to store beetles dissipated within 24 h. Because the sex and size of

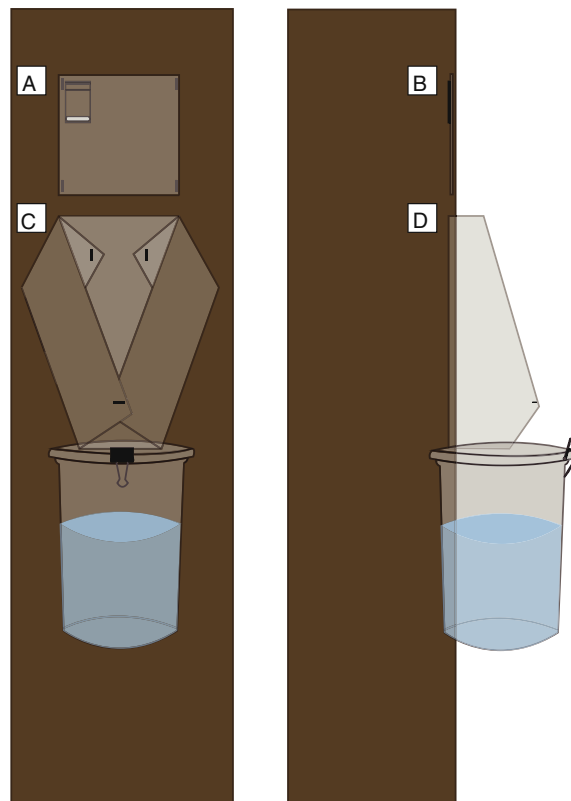


Figure 1 Design of the two types of traps and their relative positions on tree trunks. (A, B) Sticky traps were constructed of transparent plastic sheets coated with adhesive, stapled to the tree, with attached pheromone lure. (C, D) Bucket traps were constructed of transparent acetate sheets attached to a plastic container that was filled with water (blue), and were positioned below sticky traps to capture insects that had escaped.

individuals can influence response by conspecifics, each beetle was sexed and had its body size estimated by measuring the length of the right elytron. Male beetles used as visual cues in our study were larger than females ($\chi^2 = 3.96$, d.f. = 1, $P = 0.05$), with a mean (\pm SE) right elytron length of 1.07 ± 0.03 cm compared to a mean female elytron length of 0.98 ± 0.03 cm. On each sticky trap, one dead beetle was randomly selected and stuck to its center as a visual cue (total: 24 female, 19 male beetles). Post hoc analysis confirmed that the number of *M. caryae* captured was not associated with the estimated body size of the visual cue (Kruskal–Wallis test: $\chi^2 = 3.93$, d.f. = 6, $P = 0.69$). Pheromone lures consisted of transparent polyethylene sachets (press-seal baggies, Bagette model 14770, 5.1×7.6 cm, 0.05 mm wall thickness; Cousin Corporation, Largo, FL, USA) that were loaded with 0.5 mg of citral (Sigma Aldrich, St. Louis, MO, USA) in 1 ml of isopropanol and contained a cotton roll (#2, 3.81×0.75 cm; Patterson Dental Supply, Saint Paul, MN, USA) to prevent leakage. Control lures contained 1 ml of neat isopropanol. Lures were stapled in the upper left hand corner of sticky traps (Figure 1A).

The 90 trees selected for our study were randomly assigned to six treatments ($n = 15$ trees per treatment) that represented all combinations of the olfactory and visual cue treatments as well as controls, as follows: (1) blank trap; (2) control lure alone; (3) dead beetle alone; (4) pheromone lure alone; (5) control lure + dead beetle; and (6) pheromone lure + dead beetle. The experiment was conducted from 30 April to 5 May 2015. Our hypothesis would be supported if traps baited with both pheromone and dead beetles captured more beetles than our other treatments. Captured cerambycids were identified following Lingafelter (2007). Trees assigned to the six treatments did not differ significantly in diameter at breast height (DBH; overall mean \pm SE = 32.4 ± 0.81 cm, range: 14.7–74.4 cm; Kruskal–Wallis test: $\chi^2 = 5.37$, d.f. = 5, $P = 0.37$; Table S1) or position within the forest relative to distance from the nearest edge (45.3 ± 2.8 m, range: 7.9–106 m; $\chi^2 = 1.37$, d.f. = 5, $P = 0.93$).

Statistical analysis

Due to rain and wind damage during part of our experiment, some bucket traps were knocked off of trees. We thus excluded one blank, one adult alone, one adult + control lure, one pheromone lure, and two control lure bucket traps from our analysis, bringing our total sample size for bucket traps to $n = 84$.

Data were analyzed in R v.3.23 (R Core Team, 2015). Data were fit to the negative binomial distribution based on the recommendations of Zeileis et al. (2008) and Zuur et al. (2009), based on the variance being more than $10\times$

the mean, and the dependent variable (numbers of beetles caught per trap) being strongly left skewed and resistant to normalization by any transformation. The test for differences between treatment means was a general linear hypothesis–multiple comparisons procedure with a Tukey honestly significant difference correction (glht multcomp package; Hothorn et al., 2008; Bretz et al., 2010). The influence of tree DBH and distance to the nearest forest edge on trap catch was tested with the log-link function (glm.nb lme4 package; Bates et al., 2015) (Zuur et al., 2009). We generated confidence intervals by taking the exponent of the results produced by the confidence interval function (confint MASS package; Venables & Ripley, 2002).

Results

In total 224 cerambycid beetles were captured by traps during the study, with 216 beetles (97%) being the target species *M. caryae*, of which 155 were males and 61 were females (sex ratio: 2.5 male:female). Other cerambycids captured included one, two, two, and three adults of *Astylopsis macula* (Say), *Cyrtophorus verrucosus* (Olivier), *Phymatodes testaceus* (L.), and *Stenosphenus notatus* Olivier, respectively.

The number of adult *M. caryae* trapped was influenced by treatment ($\chi^2 = 52.13$, d.f. = 5, $P < 0.001$), with few beetles caught by blank traps or those baited only with a dead beetle, significantly more attracted to traps baited only with pheromone, but the combination of pheromone and dead beetles attracted most beetles (Figure 2). When a female beetle was included as a visual cue, traps captured more beetles (Kruskal–Wallis test: $\chi^2 = 5.82$, d.f. = 1,

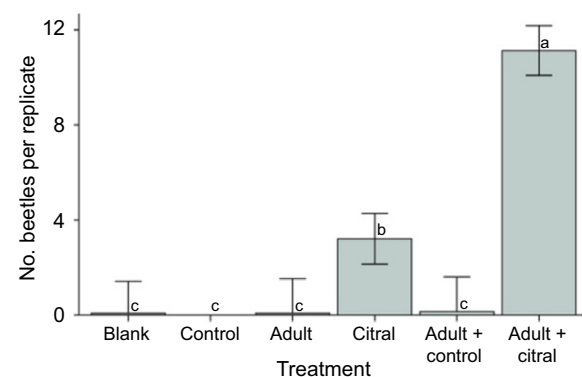


Figure 2 Mean (\pm SE) number of adults of *Megacyllene caryae* per trap by treatment. Means capped with different letters are significantly different (general linear hypothesis test: $P < 0.05$).

Table 1 Generalized linear model output for number of adult *Megacyllene caryae* captured by treatment, distance from forest edge, and shagbark hickory tree diameter at breast height (DBH)

| Treatment | Estimate \pm SE | z | Pr(> z) |
|--------------------|-------------------------------|-------|----------|
| Intercept (blank) | -3.3 \pm 0.0 | -2.48 | 0.01 |
| Beetle | -0.06 \pm 1.46 | -0.05 | 0.96 |
| Solvent | -3.4 \pm 1.86 $\times 10^7$ | 0.00 | 1.0 |
| Citral | 3.35 \pm 1.07 | 3.14 | <0.01 |
| Beetle + solvent | -0.02 \pm 1.5 | -0.17 | 0.99 |
| Beetle + citral | 4.82 \pm 1.04 | 4.60 | <0.001 |
| Distance from edge | 0.02 \pm 0.01 | 2.26 | 0.02 |
| Tree DBH | -0.01 \pm 0.02 | -0.03 | 0.97 |

$P = 0.02$), but did not change the sex ratios of captured beetles. The eight adults of other cerambycid species that were captured during the study were scattered across treatments.

The number of beetles caught by traps was not influenced by the DBH of the tree (GLM: $z = -0.03$, d.f. = 80,73, $P = 0.97$; Table 1), but trap catch increased with the distance of trees from the forest edge (GLM; $z = 2.26$, d.f. = 80,73, $P = 0.02$; Table 1). The log-likelihood of detecting *M. caryae* increased from 1.43 to 2.44 as

traps were placed on trees from 0 to 100 m into the forest (Figure 3). Transforming these values from a log scale, this difference is ca. 4 beetles per trap at 0 m and ca. 11 beetles per trap at 100 m. The dependent variable (number of *M. caryae* captured) and independent variables (DBH of tree, distance to edge, treatment) were not correlated with each other (pairs function: $P > 0.05$).

Discussion

Visual cues increase attraction to pheromones and are important for the location of mates by *Megacyllene caryae*

When presented alone, visual cues did not attract any *M. caryae* in our study, but increased attraction to citral by *M. caryae* when presented in combination. This suggests that visual cues are important for the location of mates by *M. caryae*, but only serve as an attractant after citral has been detected, either during flight, or at short ranges after or just prior to landing on host trees.

We found that the inclusion of a female beetle as our visual cue increased the number of *M. caryae* caught in our traps. Females of *M. caryae* have much shorter antennae than males and, thus, it is possible that conspecifics can identify female *M. caryae* in flight and preferentially orient toward them. This result may also be an artifact of our

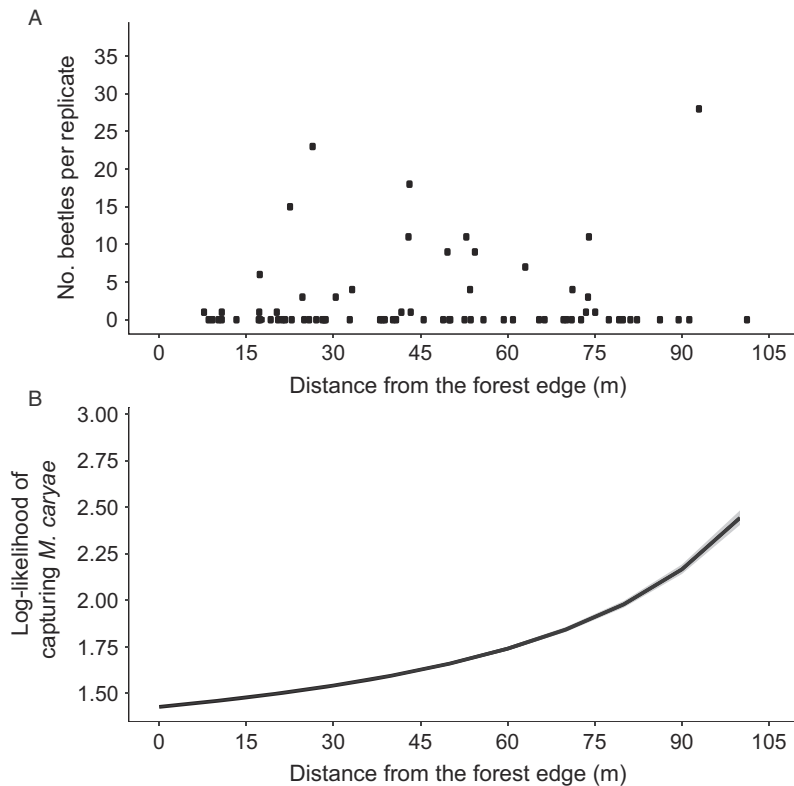


Figure 3 The relationship between the position of traps in forests and trap capture of adults of *Megacyllene caryae*. (A) Number of beetles per replicate vs. distance (m) of trap from the forest edge. Each point represents the number of beetles in a single replicate of a treatment. (B) Log-likelihood of capturing adults on hickory trees (i.e., likelihood of detecting the species) vs. distance (m) from the forest edge. The gray lines indicate two standard deviations for detection of beetles.

random assignment of beetles to treatments, as 13 out of the 15 beetles that were randomly assigned to the adult + pheromone lure treatment were female. Future work should examine whether adults of *M. caryae* are able to distinguish between male and female conspecifics while in flight. And if so, additional work should investigate whether the sex of a single beetle, or the sex ratio of many beetles within an aggregation, influences the decision of an adult *M. caryae* to land.

Because many species of beetles in the family Cerambycidae use similar or identical blends of pheromones, orientation to the incorrect species of beetle is a potential problem (Millar & Hanks, 2017). The evolution of blends of pheromones that include minor components (i.e., compounds in the blend of pheromones that are not attractive when presented alone; Mitchell et al., 2015) may be one way cerambycids that are active during the same times of day or year, avoid errors in orientation. Our findings suggest that visual cues may act as another mechanism by which beetles in sympatry avoid orientation to the wrong species of beetle.

Location of traps within a forest may influence likelihood of detecting *Megacyllene caryae*

Our study found that traps that were placed at greater distances within the interior of the forest had a higher likelihood of capturing *M. caryae*, compared to traps placed closer to the edge of the forest. Allison et al. (2019) found a similar result for three cerambycid species in the subfamily Cerambycinae, with significantly higher numbers of beetles captured at 30 m within the interior of forests at their study sites. This contrasts with research on the congener *Megacyllene robiniae* Forster, which found that *M. robiniae* was more abundant closer to the edges of forests (Harman & Harman, 1987; McCann & Harman, 1990). Because we did not sample across multiple sites, and did not sample systematically at known points inside and outside the forest, it is difficult to determine whether our result is indicative of a true pattern for *M. caryae*, or is simply representative of contextual factors (e.g., clumps of stressed trees) at our field site. Additional research should examine whether *M. caryae* are more abundant in the interior of the forest, as well as whether this is a general pattern for cerambycine species.

Potential applications to increase detection of insects of management concern

Our results may provide insight for detection of insects that are at low abundances. In order to accurately determine the range(s) of insects that are rare and/or of conservation concern, or potentially invasive and

newly introduced into a location, surveys that are often time-intensive, logistically challenging, and costly are necessary to determine the abundance of individuals within populations, as well as their geographic extents (e.g., Haack et al., 2010; Ray et al., 2014). Results from these surveys are often used to determine the status of populations and subsequent management (i.e., extent of eradication programs for non-native species; determining whether populations of endangered insects have increased or decreased in abundance). Although pheromones alone can be attractive to many beetles in the Cerambycidae (Millar & Hanks, 2017), it is possible that, when presented with an additional visual cue such as a dead beetle of the same species, trap captures, or detection of target species may be increased beyond the pheromone alone. This may indicate that it is possible to increase detection of target insects when the full pheromone blend of the target is not known, or if other environmental factors limit detection.

Conclusions and future directions

Our results confirm that the most important signal for the location of mates by *M. caryae* is its aggregation-sex pheromone, but that visual cues are also important at short ranges. Although we detected no chemicals associated with *M. caryae* on the dead beetles we used as visual cues, it is possible that residual chemicals were still present at levels not detectable by SPME. Future research should confirm specificity of response to visual cues by *M. caryae* and other species of cerambycids and short and long ranges with models produced by 3D-printing or bioreplication on the nano-scale (e.g., Domingue et al., 2014). Synthetic models can allow the independent evaluation of a number of morphological differences between and within species of cerambycids. Characteristics such as the size and shape of a beetle can be scaled to study their role in attraction, in addition to the inclusion or removal of structural features that are difficult for humans to evaluate (e.g., cavities, ridges along the elytra), but that may significantly affect the response of target insects. The aforementioned techniques, along with additional studies evaluating responses by *M. caryae* to specific patterns or colors, will contribute to a better understanding of the visual system of *M. caryae*, as well as provide baseline data for future studies investigating the role of vision or visual cues in orientation by cerambycid beetles.

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References

- Allison J, Strom B, Sweeney J & Mayo P (2019) Trap deployment along linear transects perpendicular to forest edges: impact on capture of longhorned beetles (Coleoptera: Cerambycidae). *Journal of Pest Science* 92: 299–308.
- Bates D, Machler M, Bolker B & Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Bretz F, Hothorn T & Westfall P (eds.) (2010) *Multiple Comparisons using R*. CRC Press, Boca Raton, FL, USA.
- Candolin U (2003) The use of multiple cues in mate choice. *Biological Reviews* 78: 575–595.
- Cardé RT (2014) Defining attraction and aggregation pheromones: teleological versus functional perspectives. *Journal of Chemical Ecology* 40: 519–520.
- Domingue MJ, Lakhtakia A, Pulsifer DP, Hall LP, Badding JV et al. (2014) Bioreplicated visual features of nanofabricated buprestid beetle decoys evoke stereotypical male mating flights. *Proceedings of the National Academy of Sciences of the USA* 111: 14106–14111.
- Endler JA (1992) Signals, signal conditions, and the direction of evolution. *American Naturalist* 139: S125–S153.
- Fukaya M, Akino T, Yasuda T, Yasui H & Wakamura S (2004) Visual and olfactory cues for mate orientation behaviour in male whitespotted longicorn beetle, *Anoplophora malasiaca*. *Entomologia Experimentalis et Applicata* 111: 111–115.
- Fukaya M, Akino T, Yasui H, Yasuda T, Wakamura S & Yamamura K (2005) Effect of size and color of female models for male mate orientation in the white spotted longicorn beetle *Anoplophora malasiaca* (Coleoptera: Cerambycidae). *Applied Entomology and Zoology* 40: 513–519.
- Ginzel MD & Hanks LM (2005) Role of host plant volatiles in mate location for three species of longhorned beetles. *Journal of Chemical Ecology* 31: 213–217.
- Haack RA, Hérard F, Sun J & Turgeon JJ (2010) Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. *Annual Review of Entomology* 55: 521–546.
- Hanks LM & Wang Q (2017) Reproductive biology of cerambycids. *Cerambycidae of the World: Biology and Pest Management* (ed. by Q Wang), pp. 133–159. CRC Press, Boca Raton, FL, USA.
- Harman DM & Harman AL (1987) Distribution pattern of adult locust borers (Coleoptera: Cerambycidae) on nearby goldenrod, *Solidago* spp. (Asteraceae), at a forest-field edge. *Proceedings of the Entomological Society of Washington* 89: 706–710.
- Hebets EA & Papaj DR (2005) Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57: 197–214.
- Hothorn T, Bretz F & Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal* 50: 346–363.
- Lacey ES, Moreira JA, Millar JG & Hanks LM (2008) A male-produced aggregation pheromone blend consisting of alkanediols, terpenoids, and an aromatic alcohol from the cerambycid beetle *Megacyllene caryae*. *Journal of Chemical Ecology* 34: 408–417.
- Lingafelter SW (2007) *Illustrated Key to the Longhorned Wood-Boring Beetles of the Eastern United States*. Special Publication No. 3, Coleopterists Society, North Potomac, MD, USA.
- Linsley EG (1959) Ecology of Cerambycidae. *Annual Review of Entomology* 4: 99–138.
- Linsley EG (1964) *The Cerambycidae of North America, part V: taxonomy and classification of the subfamily Cerambycinae, tribes Callichromini through Ancylocerini*. University of California Publications in Entomology 22: 1–197.
- McCann JM & Harman DM (1990) Influence of the intrastand position of black locust trees on attack rate of the locust borer (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* 83: 705–711.
- Millar JG & Hanks LM (2017) Chemical ecology of cerambycid beetles. *Cerambycidae of the World: Biology and Pest Management* (ed. by Q Wang), pp. 161–208. CRC Press, Boca Raton, FL, USA.
- Mitchell RF, Curkovic T, Mongold-Diers JA, Neuteboom L, Galbrecht et al. (2017) Evidence that cerambycid beetles mimic vespid wasps in odor as well as appearance. *Journal of Chemical Ecology* 43: 75–83.
- Mitchell RF, Reagel PF, Wong JCH, Meier LR, Silva WD et al. (2015) Cerambycid beetle species with similar pheromones are segregated by phenology and minor pheromone components. *Journal of Chemical Ecology* 41: 431–440.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ray AM, Arnold RA, Swift I, Schapker PA, McCann S et al. (2014) (R)-Desmolactone is a sex pheromone or sex attractant for the endangered valley elderberry longhorn beetle *Desmocerus californicus dimorphus* and several congeners (Cerambycidae: Lepturinae). *PLoS ONE* 9: e115498.
- Shorrocks B (1990) Competition and selection in a patchy and ephemeral habitat: the implications for insect life-cycles. *Insect Life Cycles: Genetics, Evolution and Co-Ordination* (ed. by F Gilbert), pp. 215–228. Springer, London, UK.
- Thornhill R & Alcock J (1983) *The Evolution of Insect Mating System*. Harvard University Press, Cambridge, MA, USA.
- Ulyshen M (2016) Wood decomposition as influenced by invertebrates. *Biological Reviews* 91: 70–85.
- Venables WN & Ripley BD (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York, NY, USA.
- Wang Q (2002) Sexual selection of *Zorion guttigerum* Westwood (Coleoptera: Cerambycidae: Cerambycinae) in relation to body size and color. *Journal of Insect Behavior* 15: 676–687.

- Zeileis A, Kleiber C & Jackman S (2008) Regression models for count data in R. *Journal of Statistical Software* 27: 1–25.
- Zuur AF, Ieno EN, Walker N, Saveliev AA & Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY, USA.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Characteristics of traps, shagbark hickory trees, and *Megacyllene caryae* beetles used in this study