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Range of Attraction of Pheromone Lures and Dispersal Behavior of Cerambycid Beetles

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Abstract

Cerambycid beetles (Coleoptera: Cerambycidae) can locate suitable hosts and mates by sensing pheromones and plant volatiles. Many cerambycid pheromone components have been identified and are now produced synthetically for trap lures. The range over which these lures attract cerambycids within a forest, and the tendency for cerambycids to move out of a forest in response to lures, have not been explored previously. We conducted two field experiments using baited and unbaited panel traps in northern Delaware to investigate these questions. Within forest fragments, unbaited traps that were 2 m from a baited trap captured more beetles than unbaited control traps, suggesting increased cerambycid activity leading to more by-catch in unbaited traps at 2 m from the pheromone source. Traps at further distances from a baited trap did not catch significantly more beetles than equivalent controls. In contrast, male *Prionus laticollis* (Drury), which were attracted by the likely female-produced sex pheromone 3,5-dimethyldodecanoic acid, were rarely collected in unbaited traps at any distance from baited traps. Outside the forest, baited traps attracted significantly more cerambycids than unbaited traps at distances up to 40 m from the forest edge, with catch generally decreasing between 8 and 40 m from the forest. Some cerambycids were collected in both baited and unbaited traps at all distances from the forest edge, indicating that at least some species dispersed out of the forest independent of any pheromonal attractants. Our results provide context to previous studies that used these pheromone lures, and offer insights into cerambycid dispersal behavior.

Key words: Cerambycidae, movement, forest fragmentation, *Xylotrechus colonus*, *Prionus laticollis*

Longhorned beetles (Cerambycidae) are often abundant and diverse in North American forest ecosystems, with ~1,100 species in North America and >35,000 described species worldwide (Yanega 1996, Švácha and Lawrence 2014). Larvae of most cerambycid species feed within dead wood and aid in decomposition and nutrient cycling (Linsley 1959); however, some species infest living trees, cut timber, or wooden structures, and thus are of economic concern (Solomon 1995). Larvae typically require 1–3 yr to complete development, overwintering as larvae or prepupae. Adults of most species emerge over a period of a few to several weeks in spring and summer (Hanks et al. 2014, Handley et al. 2015). Adults usually live for no more than one to two months (Yanega 1996). Mate location is often mediated by volatile aggregation pheromones produced by males of species in the subfamilies Cerambycinae, Lamiinae, and Spondylidinae, or female-produced sex pheromones for species in the subfamilies Prioninae and Lepturinae (reviewed by Millar and Hanks 2016). Attraction of both sexes to aggregation pheromones may be synergized by host plant volatiles, but the female-produced sex pheromones likely serve as the primary attractant for males (Millar and Hanks 2016).

Male-produced aggregation pheromones have been identified for a number of cerambycid species, and synthesized for use as baits in traps (e.g., Hanks and Millar 2013, Hanks et al. 2014, Handley et al. 2015, Ray et al. 2015, reviewed by Millar and Hanks 2016). Cerambycid pheromones are often highly conserved among related species, with interspecific attraction minimized through temporal and phenological isolation (Hanks et al. 2014, Mitchell et al. 2015, Millar and Hanks 2016). Pheromones of species in different subfamilies tend to be of different chemical classes, and in general do not interfere with one another, so that blends of cerambycid pheromone components can effectively attract a wide range of species, without substantial inhibition of attraction (e.g., Hanks et al. 2012, Wong et al. 2012). To further enhance attraction of many cerambycid species, plant volatiles (particularly ethanol and α-pinene) can be deployed with pheromone lures, often resulting in larger and more diverse catches than those from pheromone lures alone (Hanks et al.

2012, Millar and Hanks 2016). Ethanol is produced by a variety of woody plants when stressed (Kimmerer and Kozlowski 1982; Gara et al. 1993; Kelsey 1994, Kelsey and Joseph 2003, Kelsey et al. 2014), and α-pinene is a common plant volatile, particularly from conifers (Hanks et al. 2012, Millar and Hanks 2016). In previous studies, ethanol enhanced attraction of some cerambycid species to pheromones (Hanks et al. 2012, Hanks and Millar 2013, Handley et al. 2015, reviewed in Millar and Hanks 2016). Racemic 3,5-dimethyldodecanoic acid ("prionic acid"), a female-produced sex pheromone for a number of species in the genus *Prionus* (Prioninae), can also be included in lures to attract a variety of species within that genus (Barbour et al. 2011, Millar and Hanks 2016).

Research on dispersal of cerambycids has produced varying results, likely because of the diverse life histories of species within the family (Hanks 1999). For example, research on the dispersal of the cerambycine *Cerambyx welensii* Küster found that the majority of adults were sedentary, but dispersed an average of 200 m when they did move (Torres-Vila et al. 2013). In contrast, the lamiine *Monochamus alternatus* Hope was found to disperse only up to 37 m in a mark–recapture experiment (Togashi 1990). Overall, the scale and frequency of dispersal can be widely variable among cerambycid subfamilies and species, and should be assessed on a species-by-species basis; studies thus far have only assessed a few species (Holland et al. 2004).

In order to use pheromone- and ethanol-baited traps to study cerambycid dispersal, we must first understand the response of cerambycids to these traps. Whereas a variety of traps have been used to catch cerambycids and other saproxylic beetles, among the most effective are intercept designs such as funnel traps and cross-vane panel traps, especially those with a dark silhouette and with the surface treated with a slippery substance such as Fluon (De Groot and Nott 2001; McIntosh et al. 2001; Morewood et al. 2002; Graham and Poland 2012; Graham et al. 2010, 2012; Allison et al. 2016). When baited appropriately, such traps can catch large numbers of a diverse array of cerambycids (e.g. Hanks and Millar 2013, Handley et al. 2015, Collignon et al. 2016).

While such traps are useful to assess diversity and collect species that could otherwise be difficult to locate, their overall efficacy has yet to be assessed. In particular, the range over which a baited trap attracts cerambycids generally is not known for male-produced aggregation pheromones, and probably varies by species. In addition, traps without pheromone baits, or baited only with isopropyl alcohol as a solvent control, do collect some cerambycids (e.g. Handley et al. 2015), but it is not known whether nearby pheromone sources increase the incidence of trap catch in unbaited traps. Thus, in our first experiment, we aimed to more precisely determine the range over which cerambycid activity is affected by a blend of male-produced aggregation pheromones. Our second experiment sought to gauge the tendency of cerambycids to disperse from forest fragments, both in response to pheromones and by random movement. This dispersal tendency is especially important in the context of the highly fragmented forests prevalent in the coastal eastern United States, where our research took place.

Materials and Methods

Study Sites

Study sites were part of the FRAME (Forest Fragments in Managed Ecosystems) system, a collaboration between the University of Delaware and the U. S. Forest Service that aims to better understand urban and suburban forest fragment dynamics to improve ecosystem

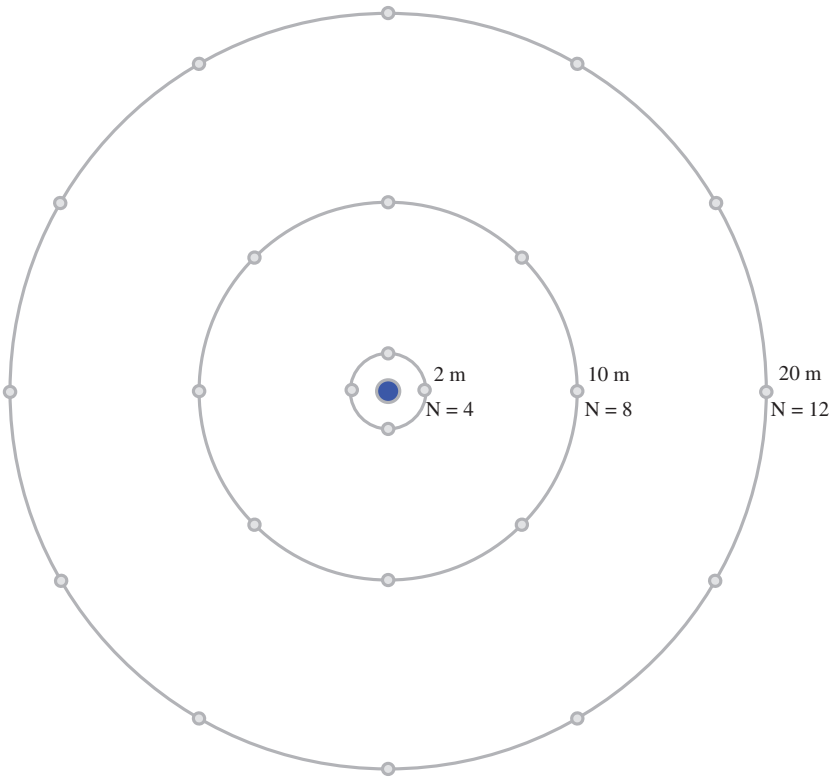

Fig. 1. Arrangement of traps for pheromone range experiment in 2014. Traps were positioned in concentric circles around a central trap at distances of 2 m ($N = 4$), 10 m ($N = 8$), and 20 m ($N = 12$). At each site, the central trap of one array was baited with synthetic pheromone, whereas all other traps were unbaited.

management (http://sites.udel.edu/frame/, Accessed 22 Jul 2016). The first experiment was conducted within two FRAME forest fragments (Folk, N 39.645670° W 75.757717°, and Glasgow 1, N 39.610898° W 75.726217°), and the second was conducted at two other FRAME sites (Ecology Woods, N 39.662422 W 75.744392°, and Glasgow 2, N 39.613133 W 75.732901°; all in New Castle County, DE). These four sites are classified as North Atlantic hardwood forests, and range in area from 16 ha (Ecology Woods) to 150 ha (Folk). High-resolution aerial photographs available online (GeoExplorer 2016) allowed us to determine a minimum age of 80 yr for forests whose canopies were closed in 1937, the date of the oldest photographs. The only site younger than this was Glasgow 1; the canopy of this site closed between 1970 and 1980, making it ~45 yr old at present.

Pheromone Range Experiment

Traps were deployed from 22 May to 26 August 2014. Within each site, two arrays of traps were established (Fig. 1), each with a central trap surrounded by concentric rings of unbaited traps at distances of 2 m (4 traps), 10 m (8 traps), and 20 m (12 traps), for a total of 24 unbaited traps. Adjacent traps 2 m away from the center were 2.8 m apart, those 10 m away were 7.7 m apart, and those 20 m away were 10.4 m apart.

At each site, one array had the central trap baited with pheromone (henceforth referred to as the pheromone array), while the other array had the central trap unbaited (the control array). From center to center, pheromone and control arrays were separated by 158 m at Folk and 112 m at Glasgow 1. Treatments were switched between pairs of trap arrays (within study sites), i.e. the center baited trap was moved to the control array and the center control trap was moved to the pheromone array, at intervals of 4.5 wk, resulting in three sampling trials. These were treated as temporal replicates, because even though species and population numbers changed over time, our aim was to determine the spatial range at which cerambycid activity in general is affected by a pheromone lure. Such replication is acceptable as long as control treatments are included during each time period (Hurlbert 1984).

We used black cross-vane panel traps (corrugated plastic, 1.2 m high by 0.3 m wide, Alpha Scents Inc., West Linn, OR) coated with Fluon (Insect-a-Slip, Bioquip Products, Rancho Dominguez, CA). Traps were hung from L-shaped frames constructed of 1.5-cm-i.d. polyvinyl chloride pipe, with a 2-m-tall upright connected with a T-fitting to a 20-cm-long arm; the trap was suspended from a loop of wire at the end of this arm. The frame upright was mounted on a 1.5-m section of steel reinforcing bar (1.0 cm in diameter) that was hammered into the ground. Beetles were captured alive by replacing the supplied collection jars with 1.89-liter plastic jars (General Bottle Supply, Los Angeles, CA) with the bottom cut out and replaced with fiberglass screen (New York Wire, Grand Island, NY) to allow precipitation to drain and air to circulate. Jars were joined to 20.3-cm-diameter funnels (US Plastic Corp., Lima, OH) that were attached to trap bottoms. Nonbiodegradable plastic packing peanuts (~2.5 cm; CPI Packaging, Inc., Somerset, NJ) were placed in a thin layer in each jar as a neutral substrate on which collected beetles could climb and conceal themselves.

Pheromone lures consisted of transparent low-density polyethylene press-seal sachets (5.1 by 7.6 cm, 0.05 mm wall thickness, Cousin Corp., Largo, FL) that were suspended in trap centers using binder clips. The synthetic pheromone blend was similar to that of previous studies (Handley et al. 2015), and formulated to contain 25 mg of each isomer per 1 ml of solvent carrier (91% isopropanol) per lure of the following compounds: racemic 3-hydroxyhexan-2-one (50 mg/lure), 2-(undecyloxy)ethanol (= monochamol, 25 mg), racemic (*E*)-6,10-dimethylundeca-5,9-dien-2-ol (fuscumol) and (*E*)-6,10-dimethylundeca-5,9-dien-2-yl acetate (fuscumol acetate; 50 mg each), all from Bedoukian Research (Danbury, CN), *syn*-2,3-hexanediol (50 mg; synthesized as described by Lacey et al. 2009), and racemic 2-methylbutan-1-ol (50 mg; Sigma-Aldrich, St. Louis, MO). These components have been shown in previous studies to attract cerambycines (Mitchell et al. 2013) and lamiines (Mitchell et al. 2011, Macias-Samano et al. 2012). Also included in the blend were citral (50 mg; Sigma-Aldrich), an isomeric blend of neral and geranial, which are pheromone components of *Megacyllene caryae* (Gahan) (subfamily Cerambycinae), and racemic prionic acid (1 mg; synthesized as described by Rodstein et al. 2009), a known sex pheromone for many species in the genus *Prionus* (subfamily Prioninae; Barbour et al. 2011). Citral has been shown to attract *M. caryae* (Wong et al. 2012), while prionic acid attracts males of several *Prionus* species (Barbour et al. 2011). Pheromone lures were replaced every 2 wk.

Central traps in the pheromone-baited arrays also contained ethanol lures consisting of ~10- by 15-cm polyethylene sachets (Cousin Corp., Largo, FL) containing 100 ml of ethanol (100%), also clipped to trap centers. Ethanol lures were monitored each week for depletion and replaced periodically throughout the summer to ensure relatively constant release rates.

Traps were set up and baited (when appropriate) on 22–23 May 2014. Traps were checked and specimens collected twice per week. We replaced used collection jars with empty ones. Specimens were returned to the laboratory and jars were frozen at ~−1 °C to kill specimens. Taxonomy of captured cerambycids for this and the next experiment follows Lingafelter (2007). Voucher specimens from

Fig. 2. Design for the dispersal experiment in 2015. Pairs of pheromone-baited and unbaited traps, separated by 5 m, were positioned every 10 m at distances of 2, 4, 8, and 40 m from the canopy edge, in random order. Three replicates were placed at each study site.

both experiments have been deposited in the University of Delaware Insect Reference Collection.

Dispersal Experiment

We used the same traps, pheromone blend lures, and ethanol lures as in the previous experiment, placing traps in open fields adjacent to two sites (Ecology Woods and Glasgow 2) from 2 June to 11 August 2015. At Ecology Woods, alfalfa dominated the majority of the field; at Glasgow 2, the field was turf in a business complex. At each site, trap pairs were spaced 10 m apart along the edge of the forest fragment at distances of 2, 4, 8, and 40 m from the dominant canopy drip line (Fig. 2). Each pair of traps included one trap baited with pheromone and ethanol, and an unbaited trap as a control. Traps within a pair were spaced 5 m apart. We placed three replicates at each site, also separated by 10 m. Within each replicate, the order of the distances was randomized but pheromone and control traps were always alternated.

Beginning 2 June 2015, traps were checked twice per week (as described above) for a total of nine collections (4.5 wk). After these nine collections, pheromone and control treatments were switched within distance treatments, providing temporal as well as spatial replicates. Trapping continued twice per week through mid-August. Traps at Ecology Woods had to be removed for 1 wk (21–28 July) to allow mowing of the alfalfa field, interrupting two collections. For this reason, we omitted this week from analysis, so that each trial lasted nine collections (4.5 wk). Specimens were collected and identified as described above.

Statistical Analyses

We conducted all analyses in R (R Core Team 2015). For each trial in both experiments, we calculated the total number of cerambycids captured by each trap to eliminate daily variation due to flight phenology or weather. Means of totals per treatment were compared by analysis of variance (ANOVA) after first confirming that data did not violate the assumptions of that test with the Shapiro-Wilk test for normality and Levene's test for homogeneity of variance. Data that violated these assumptions (*X. colonus* in the dispersal experiment) were log transformed prior to analysis, which brought them into accord with the assumptions of ANOVA. We used Tukey's HSD test to determine which combinations of pheromone treatment and distance differed from each other (McDonald 2014). Analyses were applied to total number of cerambycids, and to the two or three most abundant individual species. Treatment effects for individual species used data from the trial in which that species was most abundant, whereas for total cerambycids all trials were included as replicates.

For the pheromone range experiment, pheromone treatment and distance effects were tested with two-way ANOVAs. For the

Table 1. Taxonomy of cerambycid beetles, and numbers captured during the pheromone range experiment in 2014 by species and location, in order of abundance within subfamily

Subfamily and species	Total	Folk—Site 1	Folk—Site 2	Glasgow 1—Site 1	Glasgow 1—Site 2
Cerambycinae					
Xylotrechus colonus (F.)	828	251	173	122	282
Cyrtophorus verrucosus (Olivier)	136	46	24	30	36
Anelaphus villosus (F.)	89	23	7	15	44
Neoclytus acuminatus (F.)	29	9	5	1	14
Phymatodes testaceus (L.)	14	8	1	0	5
Neoclytus mucronatus (F.)	12	1	0	2	9
Phymatodes amoenus (Say)	4	0	1	1	2
Megacyllene caryae (Gahan)	3	2	1	0	0
Eburia quadrigeminata (Say)	1	0	0	0	1
Neoclytus scutellaris (Olivier)	1	1	0	0	0
Lamiinae					
Urographis fasciatus (Degeer)	266	47	47	67	105
Psenocerus supernotatus (Say)	147	45	20	77	5
Styloleptus biustus (LeConte)	29	9	5	4	11
Astylopsis macula (Say)	15	2	2	6	5
Liopinus misellus (LeConte)	1	0	1	0	0
Hyperplatys aspersa (Say)	1	0	0	1	0
Lepturinae					
Gaurotes cyanipennis (Say)	23	8	2	5	8
Bellamira scalaris (Say)	14	0	2	4	8
Typocerus velutinus (Olivier)	11	4	2	0	5
Necydalis mellita (Say)	10	7	1	0	2
Brachyleptura rubrica (Say)	4	1	1	1	1
Leptorhabdium pictum (Haldeman)	3	2	1	0	0
Trigonarthris proxima (Say)	2	0	1	0	1
Judolia cordifera (Olivier)	1	0	0	0	1
Strophiona nitens (Forster)	1	0	0	0	1
Trigonarthris minnesotana (Casey)	1	1	0	0	0
Typocerus lugubris (Say)	1	1	0	0	0
Prioninae					
Prionus laticollis (Drury)	158	6	45	97	10
Orthosoma brunneum (Forster)	51	21	4	7	19
Total	1,856	495	346	440	575

dispersal experiment, treatment effects were tested by a two-way ANOVA by block (replicate, including both site and trial) and distance, with pheromone and control traps analyzed separately. We also conducted paired t-tests to test the pheromone effect for each combination of site and distance treatment.

Results

Pheromone Range Experiment

We collected 1,856 cerambycid beetles of 29 species from four subfamilies during the 13.5-wk experiment in 2014 (Table 1). The majority of beetles were of the subfamily Cerambycinae (60%), followed by the Lamiinae (25%), Prioninae (11%), and Lepturinae (4%). The total number of beetles that were captured declined over the course of the season (Fig. 3), with 911, 683, and 262 beetles captured during the first trial (27 May–24 June), second trial (27 June–25 July), and third trial (29 July–26 August), respectively. The three most abundant species were the cerambycine *Xylotrechus colonus* (F.), the lamiine *Urographis fasciatus* (Degeer), and the prionine *Prionus laticollis* (Drury) (Table 1). Although *Xylotrechus colonus* was collected in greatest numbers during the first trial, it persisted throughout the season (Fig. 3). *Urographis fasciatus* showed a similar broad activity period. The flight period of *P. laticollis* was more restricted, however, with most beetles collected in July (Fig. 3).

The total number of cerambycids captured was significantly higher in the pheromone arrays than in the control arrays (Fig. 4; treatment: $F = 29.5$, df = 1, $P < 0.001$; distance: $F = 43.4$, df = 3, $P < 0.001$; treatment×distance: $F = 53.3$, df = 3, $P < 0.001$). Distance from the center affected trap catch; the interaction between treatment and distance was also significant, reflecting the lack of distance effect in the control arrays and the strong distance effect in pheromone arrays (Fig. 4). Significantly more cerambycids were collected in the unbaited traps that were 2 m from the central pheromone-baited traps compared to traps in the control arrays (mean 19.8 vs. 2.3 cerambycids per trap), but not in the unbaited traps that were 10 or 20 m from the pheromone traps (all means less than 5 cerambycids per trap; Fig. 4). Numbers of *X. colonus* and *U. fasciatus* that were collected showed similar treatment effects as those of total cerambycids (Fig. 5; *X. colonus:* treatment: $F = 13.2$, df = 1, $P < 0.001$; distance: $F = 13.7$, df = 3, $P < 0.001$; treatment×distance: $F = 19.2$, df = 3, $P < 0.001$; *U. fasciatus*: treatment: $F = 17.0$, df = 1, $P < 0.001$; distance: $F = 16.4$, df = 3, $P < 0.001$; treatment×distance: $F = 18.9$, df = 3, $P < 0.001$). However, almost all (mean 55 per trap) of the adult *P. laticollis* were collected by the

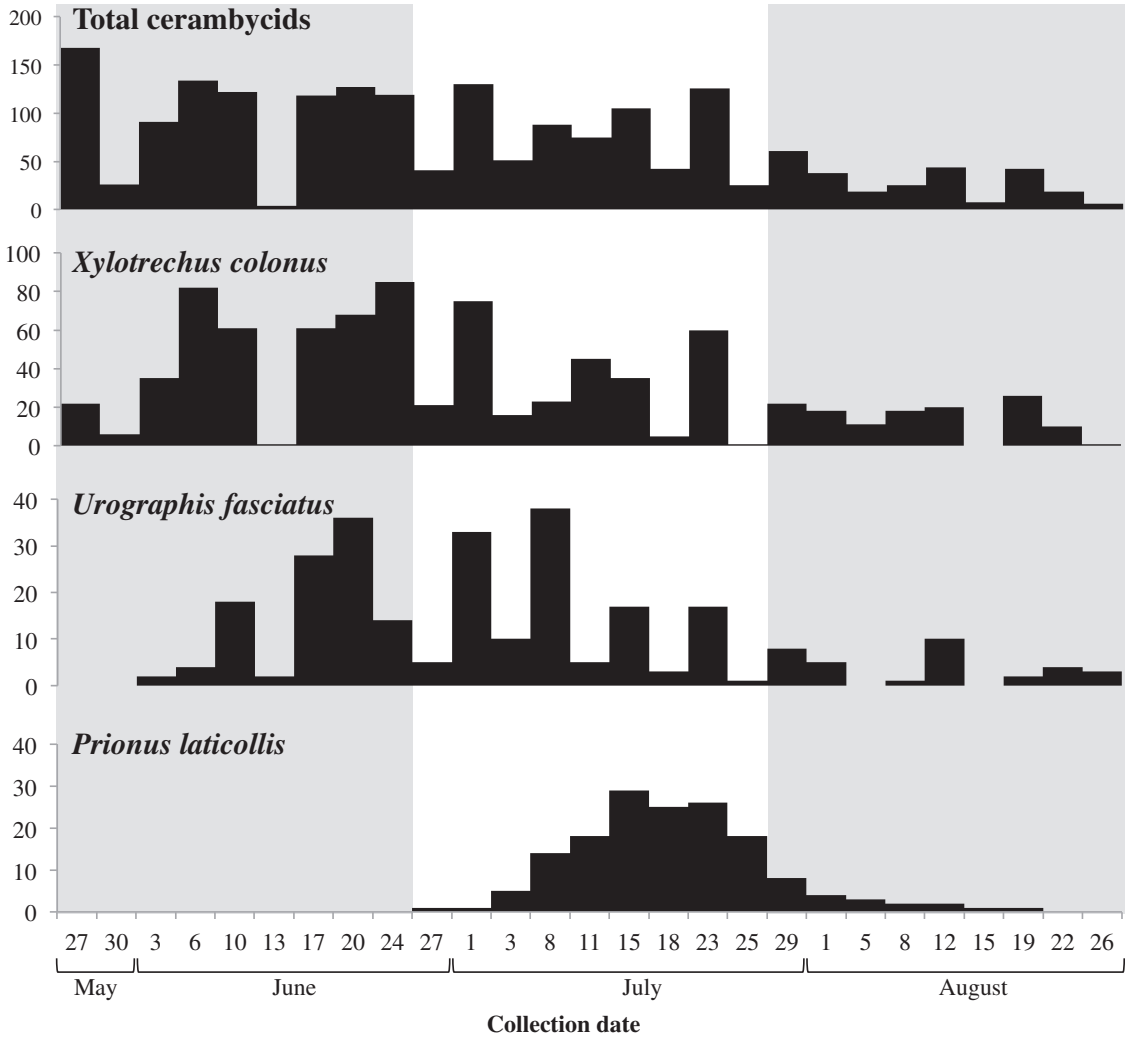

Fig. 3. Phenology of cerambycid beetles (all species combined), and the three most abundant species captured during the pheromone range experiment in 2014. Gray shading indicates the three separate trials (used as temporal replicates).

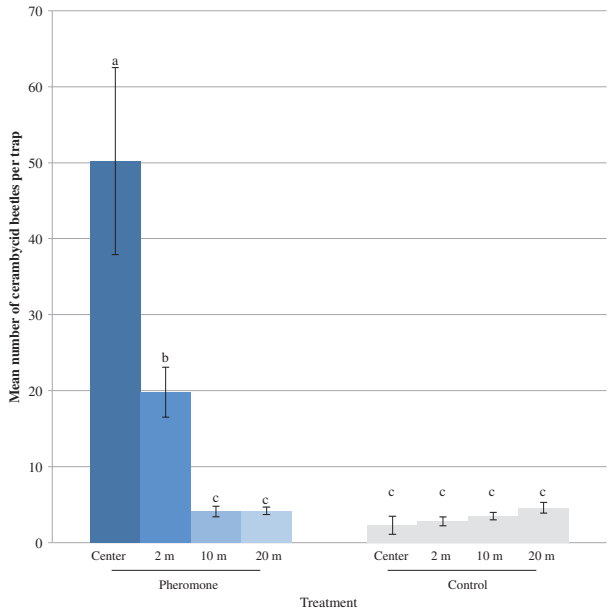

Fig. 4. Mean (± 1 SE) number of cerambycid beetles captured per trap in the pheromone range experiment in 2014 at each combination of treatment and distance from the central trap ($N = 6$, with three trials at each of two sites as replicates). Traps were placed at distances of 2, 10, and 20 m, with the central trap of one array at each site baited with synthetic pheromone, and all other traps unbaited. Letters indicate significant differences at $P < 0.05$ as determined by a two-way ANOVA and the Tukey test.

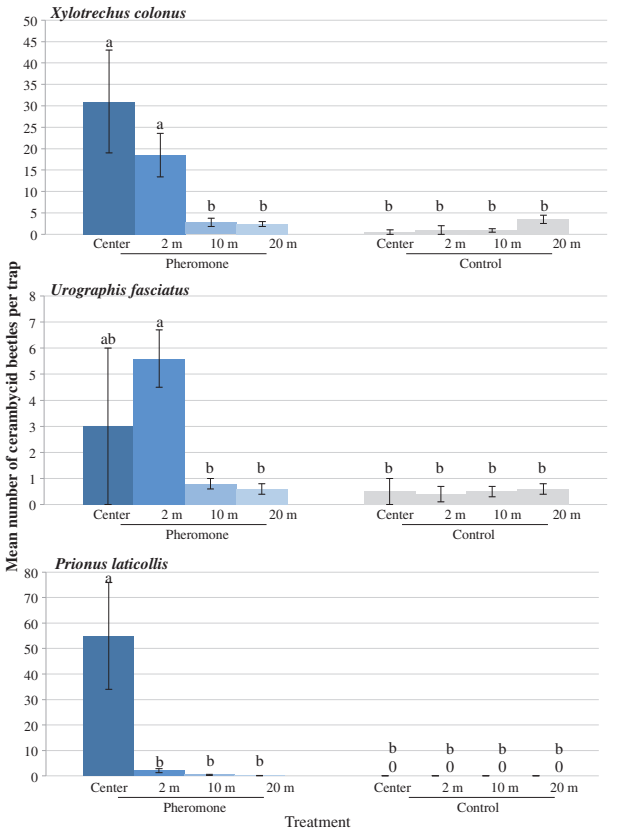

Fig. 5. Mean (± 1 SE) number of adult beetles of the three most abundant species that were captured during the pheromone range experiment by pheromone treatment and distance from the central trap. Traps were placed at distances of 2, 10, and 20 m, with the central trap of one array at each site baited with synthetic pheromone, and all other traps unbaited. Letters indicate significant differences at the $P = 0.05$ level as determined by a two-way ANOVA and Tukey test for *X. colonus*, *U. fasciatus*, and *P. laticollis*.

central baited trap (Fig. 5); very few were collected by unbaited traps 2, 10, or 20 m away (mean 2.1, 0.4, and 0.1 cerambycids per trap), and none were collected in any of the unbaited traps in the control array (treatment: $F = 18.6$, df = 1, $P < 0.001$; distance: $F = 94.5$, df = 3, $P < 0.001$; treatment×distance: $F = 94.5$, df = 3, $P < 0.001$).

Although total cerambycid catch per trap was significantly greater at traps within 2 m of the pheromone lure, cerambycids were also collected by control traps in the control array that were >100 m from a lure. Unbaited arrays collected 579 cerambycids compared to 1,275 in the baited arrays.

Dispersal Experiment

We collected 1,686 cerambycid beetles of 37 species from four subfamilies during the 9-wk experiment in 2015 (Table 2). Again, most of the beetles were of the subfamily Cerambycinae (76%), followed by Lamiinae (20%), Prioninae (4%), and Lepturinae (<1%). Total numbers of beetles collected again declined during the experiment (Fig. 6), with 1,039 and 644 cerambycids collected during the first trial (5 June–3 July) and second trial (7–11 August), respectively. *Xylotrechus colonus* was again the most abundant species captured in the traps, followed by the cerambycines *Elaphidion mucronatum* (Say) and *Neoclytus mucronatus* (F.) (Table 2; Fig. 6). As in the previous experiment, *X. colonus* peaked in June, but with continued activity throughout the summer, and *P. laticollis* activity peaked in July (Fig. 6).

Total cerambycid catch by pheromone traps decreased significantly between 8 and 40 m from the forest edge, from a mean of 31.8 per trap to a mean of 8.3 per trap (Fig. 7; all cerambycids, pheromone: $F = 8.7$, df = 3, $P < 0.001$; control: $F = 4.4$, df = 3, $P = 0.01$). A greater number of beetles was collected by the pheromone-baited traps than by their paired control traps at all distances (Fig. 7). The number of beetles captured by unbaited traps declined with distance from the forest edge, from a mean of 6 per trap at 2 m from the edge to a mean of 1.3 per trap at 40 m from the edge (Fig. 7). The number of *Xylotrechus colonus* collected showed a similar pattern, with traps at 40 m catching the fewest beetles, and unbaited traps catching few beetles regardless of distance (Fig. 7; log-transformed, pheromone: $F = 5.8$, df = 3, $P = 0.002$; control: $F = 0.9$, df = 3, $P = 0.47$). For *P. laticollis*, means for the distance treatment were not significantly different, although all captured beetles were in traps baited with pheromone (Fig. 7; pheromone: $F = 1.5$, df = 3, $P = 0.297$; control: 0 collected).

Discussion

In the pheromone range experiment, the significant decline in cerambycid collection in traps >2 m from the pheromone lure suggests that the presence of the pheromone lure caused greater activity, with beetles being intercepted when <10 m from the lure. However, other factors also may have contributed to the observed pattern of trap catches. For example, greater percentages of cerambycids may have avoided interception by outer traps while approaching the pheromone lure because those traps were spaced farther apart at 20 m than at 10 or 2 m from the central trap; thus, the range of the pheromone's attraction is likely to be larger than 2–10 m. In addition, this distance effect could also indicate that beetles do not fly at

Table 2. Taxonomy of cerambycid beetles, and numbers captured during the dispersal experiment in 2015 by species and location, in order of abundance within subfamilies

Subfamily and species	Total	Ecology woods	Glasgow
Cerambycinae			
Xylotrechus colonus (F.)	657	102	555
Elaphidion mucronatum (Say)	239	13	226
Neoclytus mucronatus (F.)	229	25	204
Sarosesthes fulminans (F.)	65	2	63
Anelaphus villosus (F.)	38	0	38
Neoclytus scutellaris (Olivier)	20	3	17
Anelaphus pumilus (Newman)	14	0	14
Neoclytus acuminatus (F.)	6	2	4
Curius dentatus Newman	6	0	6
Phymatodes amoenus (Say)	4	4	0
Cyrtophorus verrucosus (Olivier)	2	1	1
Anelaphus parallelus (Newman)	2	0	2
Eburia quadrigeminata (Say)	2	0	2
Euderces picipes (F.)	1	0	1
Smodicum cucujiforme (Say)	1	0	1
Lamiinae			
Liopinus alpha (Say)	103	12	91
Aegomorphus modestus (Gyllenhal)	77	5	72
Urographis fasciatus (Degeer)	62	5	57
Ecyrus dasycerus (Say)	25	0	25
Liopinus mimeticus (Casey)	10	0	10
Dectes sayi Dillon & Dillon	10	0	10
Liopinus misellus (LeConte)	9	5	4
Liopinus punctatus (Haldeman)	9	1	8
Lepturges confluens (Haldeman)	8	2	6
Astylopsis macula (Say)	6	2	4
Leptostylus transversus (Gyllenhal)	4	0	4
Sternidius variegatus (Haldeman)	3	1	2
Psenocerus supernotatus (Say)	2	1	1
Astylopsis collaris (Haldeman)	1	0	1
Styloleptus biustus (LeConte)	1	0	1
Lepturges angulatus (LeConte)	1	0	1
Eupogonius pauper LeConte	1	0	1
Hippopsis lemniscata (F.)	1	1	0
Lepturinae			
Bellamira scalaris (Say)	3	0	3
Typocerus velutinus (Olivier)	2	0	2
Analeptura lineola (Say)	1	0	1
Prioninae			
Prionus laticollis (Drury)	61	7	54
Total	1,686	194	1,492

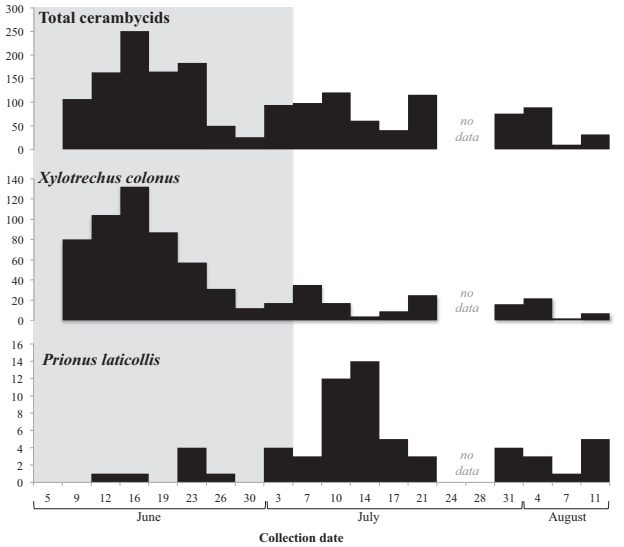

Fig. 6. Phenology of cerambycid beetles (all species combined), *Xylotrechus colonus*, and *Prionus laticollis* captured during the dispersal experiment in 2015. Gray shading indicates trial 1, unshaded area indicates trial 2 (used as temporal replicates).

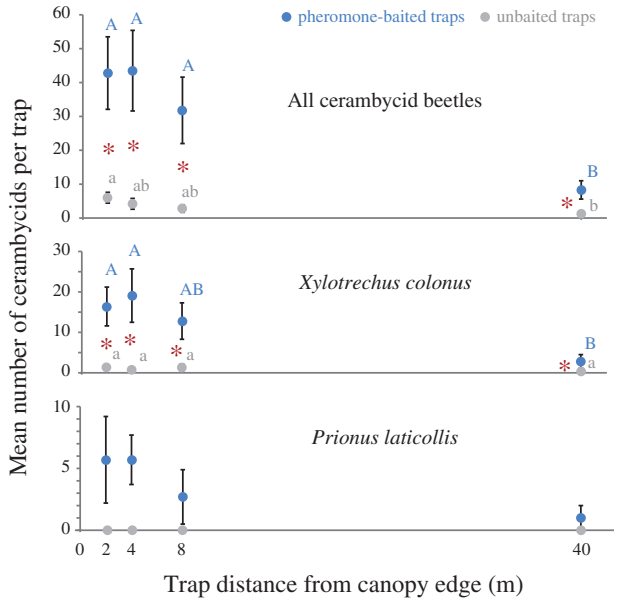

Fig. 7. Mean (± 1 SE) number of cerambycid beetles (all species combined), *Xylotrechus colonus*, and *Prionus laticollis* captured per trap in the dispersal experiment in 2015, at each distance from the canopy edge. Pairs of pheromone baited and unbaited traps, separated by 5 m, were positioned every 10 m at distances of 2, 4, 8, and 40 m from the canopy edge. Pheromone-baited and unbaited control traps were analyzed separately with blocked ANOVAs; letters indicate significant differences between means at the 0.05 level as determined by Tukey tests. Pheromone and control traps were compared at each distance using a paired one-tailed t-test; red asterisks indicate significance at $P < 0.05$.

ground level, but descend in response to the pheromone attractant. Previous research has indicated that individual species may travel at differing heights within the forest (Graham et al. 2012, Webster et al. 2016). The possible effects of these two factors could be clarified in follow-up studies using mark–recapture experiments (e.g., Drag et al. 2011, Etxebeste et al. 2013). It does appear that cerambycid trap catch in unbaited traps is affected by a nearby pheromone source, but this effect clearly declines with distance from the source.

In the dispersal experiment, the significantly greater cerambycid collection at baited traps than at paired control traps at every distance from the forest edge, even 40 m away, suggests that the range of pheromone attraction is at least 40 m. The fact that more beetles were collected near the forest edge than further in the open field suggests that most if not all were coming from the forest fragment. Similar results were found by Irmler et al. (2010), who observed a decrease in catch of cerambycid beetles at 30 m from the forest edge compared to traps along the edge, using traps baited with decaying wood.

Cerambycid species attracted by male-produced aggregation pheromones showed different patterns in our experiments than those attracted by female-produced sex pheromones, at least for the species found in high numbers in this study. *Xylotrechus colonus*

and *U. fasciatus*, both of which apparently use male-produced aggregation pheromones (Lacey et al. 2009, Mitchell et al. 2011), were collected in significant numbers at traps 2 m away from a pheromone-baited trap. In contrast, male *P. laticollis*, attracted by prionic acid, a likely female-produced sex pheromone of this species (Barbour et al. 2011), were only collected in significant numbers at the center trap containing a pheromone lure. This pattern indicates that the mechanism of attraction for *P. laticollis* is more precise than that of the species attracted by aggregation pheromones. For example, over shorter ranges, beetles responding to male-produced aggregation pheromones may also use host-related cues such as the visual silhouette presented by the panel trap to assist in locating calling conspecifics (De Groot and Nott 2001). In contrast, host-related cues may be largely irrelevant to male beetles responding to female-produced sex pheromones. A mark–recapture experiment with another prionine, *Prionus californicus* Motschulsky, estimated a maximum response range to a sex pheromone lure of at least 585 m (Maki et al. 2011). Similarly, *P. laticollis* were attracted to pheromone-baited traps outside of the forest over some distance, with no significant differences in trap catch among traps placed at distances of 2, 4, 8, or 40 m from the forest edge. Furthermore, males of this species were never collected in control traps, indicating that they were not responsive to the visual cue represented by the trap silhouette.

Many of the commonly collected cerambycid species, including *X. colonus*, are "stressed host" feeders (sensu Hanks 1999), meaning that they oviposit on trees that have been stressed by adverse environmental conditions (Hanks 1999, Millar and Hanks 2016). Stressed hosts represent a more ephemeral and sporadic resource than healthy, weakened, or dead hosts, leading to intense scramble competition both within and among species that depend on this type of resource. Hanks (1999) suggested that both male and female adults of these species should be particularly mobile, because they must seek out their unpredictable and relatively rare larval hosts. In contrast, *P. laticollis* larvae feed on living or decaying roots of a range of woody host plants. Females are sedentary and lay their eggs in the soil, while males are more mobile and seek out females for mating (Benham and Farrar 1976). For males of this species, adult females are the scarce resource, which males must locate before other males reach them (Benham and Farrar 1976, Millar and Hanks 2016). Thus, their primary if not only focus is on finding females, as adults do not feed and so have short life spans (Benham and Farrar 1976, Millar and Hanks 2016).

In the pheromone range experiment, the collection of some cerambycids in control traps more than 100 m from a pheromone lure indicates active and frequent movement of cerambycids through forest fragments. In addition, the dark silhouette of the flight intercept traps may visually attract some cerambycid species in the absence of pheromone lures, presumably because of their resemblance to a tree (De Groot and Nott 2001). This visual attraction, however, does appear to vary by individual species (De Groot and Nott 2001), and studies must consider potential confounding factors such as landing behavior and methods of collection (McIntosh et al. 2001).

We also consistently collected low numbers of cerambycids in control traps in the dispersal experiment, indicating that cerambycids were moving outside of the forest fragments; however, they may also have been lured into the vicinity due to the proximity of a baited trap 5 m away, analogous to significant numbers of beetles being collected in the 2 m traps in the pheromone range experiment. Thus, the decline in number of beetles captured by unbaited traps with increasing distance could be due to the similar decline in numbers captured by pheromone-baited traps.

Dispersal of saproxylic insects is a difficult characteristic to measure, and requires multiple methods to account for its complexity (Ranius 2006). These experiments represent a first step in understanding cerambycid movement in an urban–agricultural landscape, but future work should incorporate genetic data, mark–recapture, and other methods to complement these results.

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