SEASONAL AND DIEL PERIODICITY OF CERAMBYCID BEETLES IN EAST-CENTRAL ILLINOIS: THE POTENTIAL FOR CROSS ATTRACTION

BY

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THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Entomology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2011

Urbana, Illinois

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ABSTRACT

There appears to be considerable parsimony within the cerambycid beetle subfamily Cerambycinae in relation to pheromone biosynthesis and use. Aggregation pheromones, produced by the males, usually conform to a structural motif of a six-carbon chain with hydroxyl or carbonyl groups at C2 and C3, and closely related species often share pheromone components, or even produce pheromones of identical composition. This parsimony in pheromone structure often results in multiple species being attracted simultaneously to trap pheromone lures consisting of single synthetic chemicals. Here, I test the hypothesis that sympatric cerambycine species avoid cross attraction by differing in the subtleties of pheromone composition and/or temporal periods of activity. The research was conducted in east central Illinois with species for which pheromones already had been identified. Temporal periodicity was characterized with pheromone-baited traps equipped with a mechanism that rotated collection jars at programmable time intervals. Traps captured 1,134 beetles of eight species in three tribes of the Cerambycinae. The study strongly supported the hypothesis: 1) Species that overlapped in activity period did not share pheromone components, and so would not be cross attracted, while 2) those species that did share pheromone components were usually temporally isolated from one another, averting cross attraction.

ACKNOWLEDGEMENTS

I thank Marvin Harris for his suggestion of the use of the timer trap method, without which this thesis would never have happened. I would also like to thank my advisor Larry Hanks and committee members Andy Suarez and Marianne Alleyne for their patience, support, corrections, and good humor. Many thanks go to my fellow lab members for their invaluable help, encouragement, delicious baked goods, and wide-ranging distractions. The UIUC Department of Entomology provided an unparalleled environment for research and studies. In addition, I would like to thank the musical band Murder by Death for giving me general inspiration and a soundtrack to my life. Last but not least, I thank my family for their never-ending support and my wife, Heather Bonet, for keeping me motivated and sane over the course of my research. This project was supported by the Alphawood Foundation and the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service grant 2009-35302-05047.

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CHAPTER 1

INTRODUCTION

Insect species that are closely related often have sex pheromones that are similar in composition (Ryan 2002, Tamaki 1985). In sympatry, however, cross attraction between species may be averted by selection that favors divergence in behavior (e.g., activity period) and/or the composition of pheromones. Even subtle differences between species in pheromone composition can enforce reproductive isolation, such as has been reported in bark beetles of the genus *Attagenus* (Tamaki 1985) and moths in the genus *Ostrinia* (Klun and Huettel 1988).

Males of many species of longhorned beetles in the subfamily Cerambycinae produce volatile pheromones to which both sexes are attracted (Millar et al. 2009). There appears to be considerable parsimony within the subfamily in relation to pheromone biosynthesis and use: closely related species often share pheromone components, or even produce pheromones of identical composition (Lacey et al. 2004, 2007, 2008, 2009; Hanks et al. 2007). These pheromones usually conform to a structural motif of a six-carbon chain with hydroxyl or carbonyl groups at C2 and C3 (Millar et al. 2009). In particular, (*R*)-3-hydroxyhexan-2-one is a very common, and often sole component of the aggregation pheromones of several species (e.g., Hanks et al. 2007; Millar et al. 2009; Ray et al. 2009). The parsimony in pheromone structures often results in multiple species being attracted simultaneously to trap lures consisting of single synthetic chemicals (Lacey et al. 2004, 2007, 2008, 2009).

Here I summarize research that tested the hypothesis that sympatric cerambycine species avoid cross attraction by differing in the subtleties of pheromone composition and/or temporal periods of activity. Published information about seasonal activity period of cerambycids often is

summarized across the full geographic range of species (e.g., Yanega 1996), and so provides an inaccurate estimate for any particular area. There also is scant information on the diel, or circadian, activity periods for cerambycids (e.g., Solomon 1995). I characterized the activity patterns of cerambycid species with pheromone-baited traps that were equipped with a mechanism that rotated collection jars at programmable time intervals (see Stevenson et al. 2006). The research was conducted in east central Illinois where there are many species of cerambycines for which pheromones already have been identified (e.g., Lacey et al. 2004, 2007, 2008, 2009). Previous research has confirmed that these species are attracted to individual synthetic components of their pheromones, thus providing an opportunity for cross attraction between species that share pheromone components.

CHAPTER 2

MATERIALS AND METHODS

Beetles were captured with cross-vane panel traps (black corrugated plastic, 1.2 m tall × 0.3 m wide; model PT Intercept™, APTIV, Portland, OR) with interior surfaces treated with Fluon® to enhance trap efficiency (Graham et al. 2010). Traps were hung from L-shaped frames constructed of PVC pipe that were mounted on a section of steel reinforcing bar driven partway into the ground (see Graham et al. 2010). Traps were stabilized by attaching them with wire to three more sections of reinforcing bar driven into the ground in a circle around the trap. For each trap, I replaced the basin with a plastic funnel (~2 l, spout cut to yield a ~35-mm-diameter opening; internal surfaces treated with Fluon®) to direct captured insects into the bottle rotator. The bottle rotator (model 2850, BioQuip, Rancho Dominguez, CA) was battery powered and positioned under the trap on a section of reinforcing bar. The platen of the rotator had eight plastic bottles (~500 ml), one of which was positioned under the platen inlet and received captured insects, while the openings of the remaining jars were covered by the platen, preventing insects from escaping. The time interval for rotation of bottles was modified during the season to optimize trap catch (see below).

Traps were baited with multiple lures, each containing a different compound or blend of compounds, that together produced a bouquet of volatiles that previously had been identified as aggregation pheromones or attractants for a variety of cerambycid species (for methods of synthesis and bioassay results, see Lacey et al. 2004, 2007, 2009; Hanks et al. 2007; Millar et al. 2009; RFM, unpub. data). These compounds included the following: 1) three enantiomeric blends of compounds of the common structural motif (see Introduction): (*R**)-3-hydroxyhexan-

2-one, and either (2*R**,3*R**)-2-3-hexanediol or (2*R**,3*S**)-2,3-hexanediol (alternated at intervals to prevent inhibition: Lacey et al. 2004); 2) citral (Sigma-Aldrich, St. Louis, MO), a blend of neral and geranial which are pheromone components of the cerambycine *Megacyllene caryae* (Gahan) (Lacey et al. 2008); 3) (*R**)-2-methylbutan-1-ol, a pheromone component for some *Phymatodes* species (Hanks et al. 2007; unpub. data); and 4) (*E*)-6,10-dimethyl-5,9-undecadien-2-yl acetate, a male-produced aggregation pheromone for species of *Tetropium* (subfamily Aseminae/Spondylidinae; Silk et al. 2007) which also serves as at least an attractant for several species in the subfamily Lamiinae (RFM, unpub. data). An independent experiment conducted during the same season and in the same area revealed that none of the compounds inhibited attraction of cerambycines to the other compounds (unpub. data).

Lures were clear polyethylene bags (Bagette model 15770, 5.1 by 7.6 cm, 0.05 mm wall thickness, Cousin Corp., Largo, FL) that were loaded with 25 µl of chiral compounds, or 50 µl of racemic blends, in 1 ml of 95% ethanol. Ethanol is an efficient carrier of the compounds and has negligible if any activity for cerambycid beetles at these volumes (e.g., Hanks et al. 2007). Preliminary studies indicated that the various compounds permeate the polyethylene and evaporate at a reasonably constant rate (unpub. data). Lures lasted ~1-2 wk in the field and were replaced as needed.

Over the course of the study, two timer traps were set up in residential neighborhoods of Urbana, IL (Champaign Co.) that were at least 45 years old and had mature trees of diverse species. Earlier studies had confirmed that cerambycid species were present in these urban habitats (Lacey et al. 2004, 2007, 2008; RFM, unpub. data). One trap remained at a single site throughout the season (Study site 1; 5 April - 14 August 2010; 40.097057N, -88.203135W), whereas the location of the other trap was changed in late spring due to poor trap catch (initial

study site, 12 April - 6 May: 40.073603° N, -88.208193° W; second study site, 22 May - 9 August 2010: 40.107385N, -88.198476W). These traps were initially programmed to rotate bottles at hourly intervals from 10:00 to 20:00 h, then every two hours between 20:00 - 10:00 h. I later discovered that very few beetles were captured between 00:00 and 11:00 h (see Results and Discussion), so I subsequently assigned that time period to a single bottle (on 30 June 2010). There was a total of 1,818 separate trap events across study sites and dates during the course of the study.

For each trap, I recorded the date and time during which each beetle was captured. Study sites did not differ significantly in the mean dates and times of day on which the best represented species were captured (see Results; ANOVA $P > 0.05$ for all tests). I therefore combined data across study sites to compare seasonal and circadian activity periods of the different cerambycid species. The present publication summarizes only data for species of the Cerambycinae to test the hypothesis.

For the purposes of this study, the statistical comparison of interest is the overlap between species in the frequency distributions of date or hours of activity, so statistical tests of central tendency (e.g., ANOVA) were not appropriate. I characterized activity period for each species by calculating means and doubled standard deviations (which account for ~95% of observations). Thus, overlap in the doubled standard deviations of two species was taken as evidence of synchrony. I also include an independent assessment of temporal overlap between species using a simulation program (TimeOverlap, T. F. Rangel) based on the index developed by Czechanowski (Feinsinger et al. 1981). For that analysis, trap catch data for seasonal data were collapsed into 10-d periods, while circadian data were collapsed into 2-h periods from 12:00 to 24:00. A significant *P* value for the Czechanowski index indicates that distributions

overlap less than would be expected by chance (i.e., overlap is not significant, and species are not synchronous).

CHAPTER 3

RESULTS AND DISCUSSION

During the study, I captured 1,034 beetles of eight species in three tribes of the Cerambycinae (Table 1). Larvae of most of these species were broadly polyphagous, feeding in stressed and dying trees in several families of hardwoods, with the exception of *Phymatodes amoenus* (Say) larvae, which develop in dead grape vines (Lingafelter 2007). A clear progression of species were captured over the course of the season (Fig. 1A), beginning with *Neoclytus caprea* (Say) in early April and ending with its congener *N. mucronatus* (F.) in mid-August. Most of the species were active for only a brief period of the season, generally ~2 wk.

The estimated duration of flight period was not merely an artifact of sample size, as evidenced by the brief flight period of *Phymatodes amoenus* (Say), which was represented by nearly 500 specimens, compared to the relatively long flight period of *Xylotrechus colonus* (F.), which was estimated from less than 1/10 as many specimens (Table 1). *Neoclytus acuminatus* (F.) had the most prolonged activity period. A study of that species in Alabama (Waters 1981) attributed the long activity period to its being multivoltine. There was slight evidence of a bimodal frequency distribution for *N. acuminatus* in my study (Fig. 2), suggestive of two generations. Even if that were true, the generations overlapped broadly, and adults were active continuously throughout the entire flight period. Frequency distributions of the remaining species appeared unimodal (data not shown).

Beetle species also varied considerably in circadian rhythms of activity (Fig. 1B), independent of seasonality. Circadian rhythms were consistently associated with body color, as described by Linsley (1959a; see Lingafelter 2007 for images). For example, species in the tribe

Clytini that were active during afternoons (*N. caprea*, *N. acuminatus*, *Megacyllene caryae* [Gahan]) were brightly marked with yellow or red and black on the elytra or dorsum of the abdomen, consistent with group mimicry of stinging Hymenoptera that is a general characteristic of the tribe (Linsley 1959b). In contrast, adults of the clytines *Xylotrechus colonus* (F.) and *N. mucronatus* were active in late afternoon until well after nightfall, and were more somber in coloration. In the tribe Callidiini, the few adult *Phymatodes testaceous* (L.) that were captured (Table 1) were clearly crepuscular, while the much more abundant congener *P. amoenus* (Say) was active during late afternoon. Although both of the *Phymatodes* species are black and red in body color, the diurnal *P. amoenus* was much more vividly colored than its congener. The only strictly nocturnal species, *Elaphidion mucronatum* (Say) (tribe Elaphidiini), was mottled dark brown, consistent with the association between body color and circadian activity period.

Pheromones previously had been identified for seven of the study species, and in most cases were consistent with the hexanediol/hydroxyhexanone motif (Table 1). These pheromones are emitted by pores in the prothorax, which were present in all seven species (Ray et al. 2006; unpub. data). The pheromone of *E. mucronatum* have yet to be identified, but field trials have confirmed that both sexes are attracted to traps baited with live males, suggesting that volatile pheromone are produced (Robinson et al. 2011). Male *E. mucronatum* lack the prothoracic gland pores that are associated with production of the pheromones of the structural motif, suggesting that the structure of the pheromone may be different (also see Ray et al. 2009).

The study strongly supported the hypotheses: 1) Species that overlapped in activity period did not share pheromone components, and so would not be cross attracted; and 2) those species that did share pheromone components were usually temporally isolated from one another. For example, *N. caprea* and *M. caryae* emerged nearly synchronously and overlapped

to a lesser, but still significant extent in circadian activity period. Those two species do not share pheromone components (Table 1), and thus would not be cross attracted despite their temporal overlap. In addition, the four species that produce 3*R*-hydroxyhexan-2-one as the dominant or sole pheromone component flew at significantly different times of year: *N. caprea*, *P. amoenus*, *X. colonus*, and *N. mucronatus* (Fig. 1A). Furthermore, adults of the two species of *Phymatodes*, which share (*R*)-2-methylbutan-1-ol, were active at the same time of year, but different times of day (Fig. 1A,B).

Phymatodes amoenus is endemic to eastern North America (Monné and Bezark 2010), but *P. testaceus* is an invasive species native to Europe that is believed to have colonized North America sometime during the last century (Bense 1995; Lingafelter 2007; I. P. Swift, pers. comm.). The circadian activity period of *P. testaceous* in Europe is currently unknown, which suggests two possible explanations for the temporal difference in activity between the two species. First, the activity period of *P. testaceous* at my study site could be an artifact of selection in its native range, in which case its colonization of North America may have been facilitated by the lack of temporal overlap with *P. amoenus* (Monné and Bezark 2010). Second, selection against cross attraction in North America may have resulted in the later circadian activity period of *P. testaceus* that I observed in this study.

Cross attraction between adult *X. colonus* and *N. acuminatus* would seem to be possible, since (2*S*,3*S*)-2,3-hexanediol is a minor pheromone component of the former, and the sole pheromone component of *N. acuminatus* (Table 1). Adult *X. colonus* tended to emerge earlier in the year and fly later in the day than *N. acuminatus* (Fig. 1A,B), but temporal overlap nevertheless was significant. However, adult *X. colonus* are not attracted to (2*S*,3*S*)-2,3-hexanediol when presented alone (Lacey et al. 2009), and thus might not be attracted to calling

males of the other species. The question remains as to whether adult *N. acuminatus* would be attracted to calling males of *X. colonus*. In an earlier study (Lacey et al. 2009), significant numbers of adult *N. acuminatus* were attracted (2*S*,3*S*)-2,3-hexanediol alone, but very few were attracted by the blend of synthetic compounds that was representative of the pheromone of *X. colonus*. It should be noted, however, that the release rate of the trap lures is much higher than that of the male beetles (see Methods), so attraction to the synthetic blend could be unrealistic.

While this study has accomplished much in terms of explaining how cross attraction is avoided among sympatric cerambycine species that have similar pheromones, many questions remain. For example, the pheromone of *E. mucronatus* must be identified to determine whether there is a possibility of cross attraction with sympatric species. Also, several species in the area of my study share components with the species in Table 1 but were not captured. These species include *Anelaphus pumilus* (Newman) (pheromone composed of only [*R*]-3-hydroxyhexan-2-one; unpub. data), *Xylotrechus convergens* LeConte ([*R*]- and [*S*]-3-hydroxyhexan-2-one, [*R*]-2-hydroxyhexan-3-one; unpub. data): *Sarosesthes fulminans* (Newman) ([2*S*,3*S*]- and [2*R*,3*R*]-2,3-hexanediol; Lacey et al. 2009), and *Curius dentatus* Newman ([2*R*,3*S*]- and/or [2*S*,3*R*]-2,3-hexanediol; Lacey et al. 2004). An examination of Fig. 1 reveals many "open niches": combinations of seasonal and circadian activity periods that would offer these species temporal refuge from other species that use similar pheromones, even among species that communicate over the crowded (*R*)-3-hydroxyhexan-2-one pheromone "channel". Given the findings of the present study, it seems likely that these remaining species avert the deleterious consequences of cross attraction by differing from other sympatric species in phenology and pheromone composition.

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TABLE AND FIGURES

Table 1. Taxonomy and activity periods of cerambycid species that were captured by timer traps. Pheromone components ordered by amount that they represent of blends.

Tribe	Species	Number captured	Sex ratio (%F)	Pheromone components	Reference
Callidiini	*Phymatodes amoenus* (Say)	491	55%	3*R*-hydroxyhexan-2-one, 2*R*-2-methylbutanol	Unpub. data
	Phymatodes testaceus (L.)	3	75%	2*R*-methylbutanol	Unpub. data
Clytini	*Megacyllene caryae* (Gahan)	152	32%	neral, terpineol, geranial, 2-phenylethanol, (S)-(-)-limonene, (-)-α- nerol, 2*S*,3*R*- and 2*R*,3*S*-hexanediol	Lacey et al. 2008
	Neoclytus acuminatus (F.)	275	50%	2*S*,3*S*-hexanediol	Lacey et al. 2004
	Neoclytus caprea (Say)	21	48%	3*R*-hydroxyhexan-2-one	Unpub. data
	Neoclytus mucronatus (F.)	65	60%	3*R*-hydroxyhexan-2-one	Lacey et al. 2007
	Xylotrechus colonus (F.)	19	47%	3*R*-hydroxyhexan-2-one, 2*S*,3*S*-hexanediol, 3*S*-hydroxyhexan-2-one, 2*R*,3*R*-hexanediol	Lacey et al. 2009
Elaphidiini	*Elaphidion mucronatum* (Say)	8	43%	Evidence of pheromone[a], structure unknown	Robinson et al. 2011

[a]Adults of both sexes are attracted to traps baited with live males

Fig. 1. Temporal patterns of activity for eight species of the Cerambycinae captured by timer traps in east-central Illinois (sample sizes in Table 1): A) Seasonal variation (ordinal date of capture); B) Circadian variation (decimal hour of capture). Horizontal lines indicate means, and shaded boxes represent ± 2 SD around the mean (~95% of data points are contained within boxes). Boxes with different letters are significantly different (i.e., frequency distributions do not overlap significantly; Czechanowski index $P < 0.05$). Dotted lines separate early-, mid-, and late-season species (see Results), to facilitate interpretation of the Results.

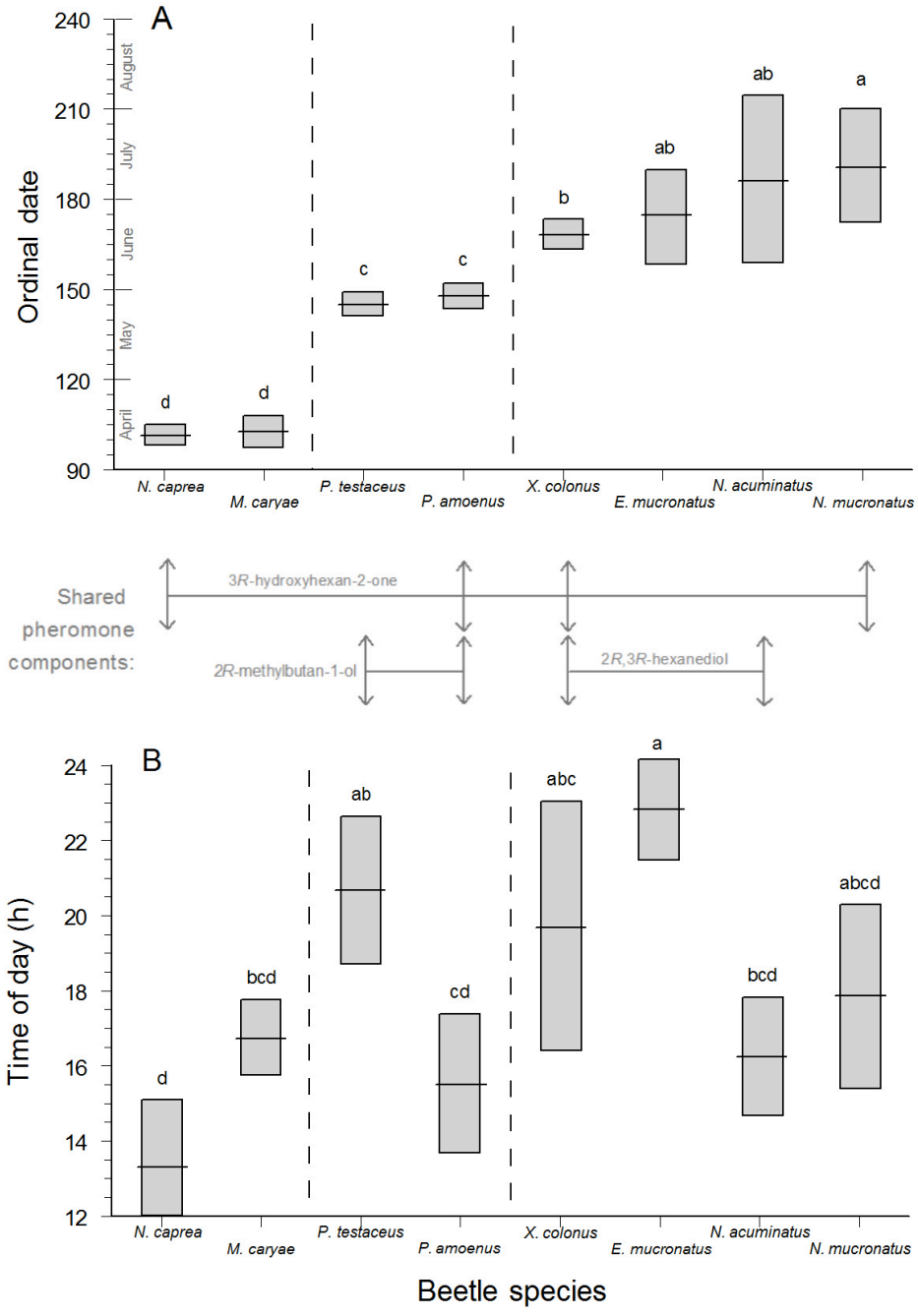

Fig. 2. Frequency distribution for number of adult *Neoclytus acuminatus* (F.) captured by timer traps in central Illinois during 2011.