HOST PLANT ASSOCIATIONS AND CHEMICAL ECOLOGY OF CERAMBYCIDAE

BY

JOSEPH CHUNG HUEN WONG

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Entomology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2016

Urbana, Illinois

Doctoral Committee:

Professor Lawrence M. Hanks, Chair, Director of Research
Professor Andrew V. Suarez
Assistant Professor Brian F. Allan
Associate Professor Matthew D. Ginzel, Purdue University

ABSTRACT

Invasive species are a major threat to forest ecosystems, threatening native biodiversity, forest health, altering nutrient cycles, and deteriorating water and soil qualities. In the United States alone, economic losses are estimated to be around $120 billion, both from impact of invasive species to the environment and in efforts to prevent and respond to them. With increasing rates of biological invasions posing a major threat to forests in the United States and worldwide, prevention of introduction of exotic species is of high importance. A number of longhorned beetle species (Coleoptera: Cerambycidae) are considered major pests worldwide. Longhorned beetles include some of the most damaging pests of woody plants and invasive species pose a serious threat to North American forests.

The beetle family of Cerambycidae is a diverse group whose larvae feed primarily in the woody parts of trees, and many species are important pests in their native regions, and when introduced into new regions. Effective detection and survey programs are increasingly important as the rate of introduction of exotic species rises with the continued growth of international trade. Semiochemicals, particularly volatile pheromones, are an effective way to attract a number of cerambycid beetles to traps. The focus of my dissertation research was to evaluate current trapping methods and potential ways of optimizing these methods. I compiled a comprehensive list of larval hosts for North American cerambycid species based on rearing records and larval gallery descriptions to gain a better understanding of potential hosts of different species of cerambycids. I present data confirming some of the pheromone components present in two cerambycine species do not act as attractants. I demonstrate that beetles' attraction to traps may be enhanced by increasing the release rates of synthesized pheromones. I show that cerambycid species varied as to whether attraction to pheromones is enhanced or inhibited by volatiles

released from larval hosts. I describe a field experiment which tested the extent to which fermenting bait composed of crushed fruit, sugars, yeast, and wood chips enhanced attraction of beetles to a blend of synthesized cerambycid pheromones, and how trap catch was influenced by the vertical position of traps within forests. Finally, I describe a morphological survey of cerambycine species using scanning electron microscopy which showed that for all 22 species, males had pores in the prothorax, absent in females, which in other cerambycids are associated with glands that produce pheromones. This finding is further evidence that use of volatile sex pheromones is common in the Cerambycidae.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION …….1

CHAPTER 2: AUTHENTICATED RECORDS OF HOST PLANT ASSOCIATIONS FOR NORTH AMERICAN CERAMBYCID BEETLES.....….....13

CHAPTER 3: AN EVALUATION OF METHODS USED FOR FIELD BIOASSAYS FOR TESTING ATTRACTION OF CERAMBYCID BEETLES TO SYNTHESIZED PHEROMONES……...…….67

CHAPTER 4: INFLUENCE OF VOLATILES FROM LARVAL HOST PLANTS ON ATTRACTION OF CERAMBYCID BEETLES TO SYNTHESIZED PHEROMONES...……93

CHAPTER 5: INFLUENCE OF FERMENTING BAIT AND VERTICAL POSITION OF TRAPS ON ATTRACTION OF CERAMBYCID BEETLES TO PHEROMONE LURES…..117

CHAPTER 6: MORPHOLOGICAL EVIDENCE OF PHEROMONE PRODUCTION IN CERAMBYCID SPECIES NATIVE TO CHINA……..138

CHAPTER 1: INTRODUCTION

Invasive species pose a major threat to many aspects of our lives. Annual economic losses in the United States from all invasive species are estimated to be around $120 billion, both from impact of invasive species to the environment and in efforts to prevent and respond to them (Pimentel et al. 2005). Many fundamental aspects of invasive species biology are still not well understood. Increasing rates of biological invasions pose a major threat to forests in the United States (Aukema et al. 2010) and worldwide. Invasive species in the United States have caused problems in forest ecosystems, threatening native biodiversity, forest health, altering nutrient cycles, and deteriorating water and soil qualities (Pimentel 2005). In addition, forests in the United States have not yet been exposed to the full range of possible invasions, or the full effects of already established exotic species. Since current and past attempts to eradicate established invasive alien species have been met with little success, prevention of the introduction of exotic species is of high importance. Despite improvements in shipping regulations, important pathways for the entry or spread of invasive species of US forests remain open or only partially regulated (Campbell 2001).

A number of longhorned beetle (Coleoptera: Cerambycidae) species are considered major pests worldwide (Linsley and Chemsak 1997). The insect family Cerambycidae is one of the largest groups of insects with over 30,000 recognized species worldwide (Slipinski et al. 2011). The larvae of these beetles are herbivorous, with most species feeding in the sap wood of trees (sometimes boring to the heart wood), and some feeding on roots, or within stems and twigs of forbs and trees (Solomon 1995). Wood-boring beetles in this family play important roles in forest ecosystems, especially as nutrient recyclers, initiating the breakdown of dead woody plants (Linsley 1959). While many species are beneficial and play a necessary part in the natural

ecosystem, some species can result in considerable economic injury, particularly in cases where larvae feed in and kill living trees, damaging stressed trees or dead wood reducing value of timber, or crops with agricultural value (Reddy 2007).

Longhorned beetles include some of the most important pests of woody plants. Invasive cerambycids pose a serious threat to North American forests (e.g., Brockerhoff et al. 2006, Haack 2006), most notably, the invasion of the Asian longhorned beetle, *Anoplophora glabripennis* Motschulsky (Haack et al. 2010), the more recent invasion of *Trichoferus campestris* (Faldermann) (National Agricultural Pest Information System 2013), and the potential invasion of *Xylotrechus rufilius* Bates (Dobesberger 2004). The life histories of these beetles, including but not limited to host range and mechanism of host location in the family is still poorly understood (e.g., see volumes indexed in Linsley and Chemsak 1997). This lack of understanding of the biology of these beetles has hindered our ability to develop effective management strategies. The need for effective surveillance methods of potential invasive species is evident, as regulatory agencies are still limited in their ability to keep out exotic cerambycids due to frequent introductions into the country (Haack et al. 2010). Detection and survey programs are important tools in preventing invasion of exotic species, as the rate of introduction of exotic species has been rising with the continued growth of international trade (Aukema et al. 2010).

The concealed nature of cerambycid larvae makes adults more reasonable to target for survey and monitoring efforts. Cerambycid beetles are trapped by a variety of methods, for example, multi-funnel traps, black lights, stovepipe traps, sticky traps, and flight-intercept panel traps (e.g., Stewart and Lam 1970, Lindgren 1983, Chénier and Philogène 1989, Czokajlo et al. 2003, Lacey et al. 2004, Bouget et al. 2008, Miller and Crowe 2011, Allison et al. 2014). Flight-

intercept panel traps have been deployed in favor of these other trap types by researchers in recent years due to their effectiveness combined with ease of use and low cost (Allison 2014). Improvements are still being made to these traps, for example, Fluon® treated flight-intercept panel traps have been shown to be much more effective than untreated panel traps in capturing cerambycids (Graham 2010, Graham and Poland 2012).

While these traps, when used primarily as passive traps, are effective for bark beetles and other woodborers, they are not as effective in capturing cerambycids without the use of attractants. The earliest baits developed for cerambycids were plant volatiles, with ethanol and monoterpenes proving to be effective attractants for many species whose larvae develop in conifers (reviewed by Millar and Hanks 2016). The list of attractants for cerambycids has grown significantly over the few decades. Male produced pheromone components, (2*S*,3*S*)-2,3-ocatanediol and 2*S*-hydroxyoctan-3-one, were identified for *Xylotrechus pyrrhoderus* in 1984, the first isolation and identification of a male sex pheromone in Cerambycidae (Sakai et al. 1984). Since then a number of beetles in the subfamily Cerambycinae have been found to have sex and aggregation pheromones, produced by males, including 3-hydroxyhexan-2-one, the analogous 2,3-hexanediols, and the homologous 8-carbon compounds. These compounds are produced by a number of species worldwide and often the sole pheromone components (Millar et al. 2009). A similar pattern is found in other subfamilies of cerambycids, most notably, (*E*)-6,10-dimethyl-5,9-undecadien-2-ol ("fuscumol") described as male-produced aggregation pheromones of the genus *Tetropium* (Spondylidinae; Silk et al. 2007, Sweeney et al. 2010) and this same chemical and its acetate were described from a species in the Lamiinae (Meier et al 2016). 2- (undecyloxy)-ethanol is the male-produced aggregation pheromone of the genus *Monochamus* (Lamiinae; Pajares et al. 2010, Teale et al. 2011). In the subfamily Prioninae, 3,5-

dimethyldodecanoic acid is a female produced sex pheromone and attractant for males of many species in the genus *Prionus* (Prioninae; Barbour et al. 2011, Rodstein et al. 2009). Additionally, many of these characterized pheromones are attractive to both sexes (e.g., Millar et al. 2009; Mitchell et al. 2011). This coupled with the remarkable parsimony that exists for pheromones within the family is advantageous for monitoring and trapping efforts, especially given that there pheromones have been effective in catching beetles worldwide. Generic lures composed of these compounds also are effective in attracting multiple species in different tribes and subfamilies, and are therefore practical for use in detecting and monitoring native and exotic cerambycids (e.g., Hanks et al. 2012; Wong et al. 2012).

The overall goal of my dissertation research was to evaluate current trapping methods and gain insight into the chemical ecology of cerambycids, in particular, volatiles that would optimize trapping methods for cerambycids. While significant progress has been made in our knowledge of cerambycid chemical ecology, particularly in our knowledge of cerambycid pheromones, much of the research regarding volatile cues that mediate host location have been focused on species whose larvae develop in gymnosperms (e.g., Sweeney et al. 2004, Ryall et al. 2014). In contrast, little progress made on volatile attractants of angiosperms hosts, with much of the research limited to laboratory studies (e.g., Hanks et al. 1996, Ginzel and Hanks 2005, Fonseca et al. 2010). I explore the role plant volatiles from damaged and fermenting materials play in attracting cerambycid beetles, especially how they may augment response to pheromone baits.

In the second chapter, I present a compiled list of larval hosts for 500+ species of cerambycid beetles in North America. Published host records often are incomplete and uncertain, especially when based in part on earlier secondary literature, and often contain scanty

information on natural history (e.g., Yanega 1996, Lingafelter 2007). Many publications include plant associations based on adults collected from plants (e.g., Linsley and Martin 1933), while this may indicate adult association with the plant, it does not provide information on larval associations. Larval cerambycids feed within plants, and do not emerge until adulthood (Švácha and Lawrence 2014), it is therefore difficult to document host associations of larvae without collecting woody materials and rearing adult beetles from their larval hosts. I examined the primary literature for data on host associations derived from rearing records, extirpation of pupae and teneral adults, and detailed descriptions of larval galleries, to clearly distinguish them from being potential adult hosts which may or may not overlap with the larval hosts.

In the third chapter, I present research that evaluates the efficacy of current methods of trapping cerambycid beetles, with the goal of optimizing trapping efficiency and gaining some insight into the basic biology of cerambycid beetles at the same time. First, I assessed the attraction of beetles to unbaited traps (its effectiveness as a visual cue or incidental trapping) and traps baited with isopropanol (the solvent commonly used to dilute synthesized pheromones), and whether isopropanol is an attractant. Second, I experimentally evaluated if traps within transects interfered with one another by intercepting beetles that are flying to another trap positioned upwind. I also determined the distance traps should be placed from one another to remove/minimize this effect. In a third experiment, I tested the hypothesis that pheromone components that were not found to be attractive to beetles may have had reduced capture rates due to competition with nearby traps baited with highly attractive dominant components. Lastly, I examined if greater number of beetles would be captured with higher release rates of pheromones. Release rates play an important role in attraction of cerambycid beetles, as few

beetles may be attracted to traps if rates are too low (e.g., Lacey et al. 2007), while effects of very high release rates are unknown.

In the fourth and fifth chapters, I used volatiles from wood and from fermentation as complements to an attractive pheromone blend to determine if the addition of these volatiles enhanced attraction. In the fourth chapter, I used chipped wood of five different species of plants, each tested separately, four angiosperms and one gymnosperm. Field bioassays demonstrated that while there are signs that volatiles from coarsely-chipped wood can play both enhancing and inhibiting roles in cerambycid attraction, more work is needed as traps baited with the wood chips alone were not effective in attracting cerambycid beetles. Similarly, in Chapter 5, fermenting baits enhanced the attraction of two cerambycid species, *Xylotrechus colonus* (F.) and *Graphisurus fasciatus* (Degeer), when presented with pheromones, but were not significantly attractive when presented without pheromones. I also found that traps in the forest understory captured the greatest number of *X. colonus* and *G. fasciatus*, whereas more adults of the cerambycine *Neoclytus m. mucronatus* (F.) were captured in the forest canopy, demonstrating an importance in the vertical position of traps.

In the last chapter, I examined beetle morphology using scanning electron microscopy to determine if cerambycid beetles from China had prothoracic gland pores. These pores are indicative of the use of long-range pheromones (Ray et al. 2006). I found gland pores in the prothoraces of adult males (and absent in adult females) in all 22 cerambycine species collected from Yunnan Province. The presence of these gland pores can be used as an indicator for pheromone production in species where the pheromone is unknown, and thus aid the pheromone identification process by refuting a false negative in cases where no volatile of note is collected in aerations.

References

Allison, J. D., B. D. Bhandari, J. L. McKenney, and J. G. Millar. 2014. Design factors that influence the performance of flight intercept traps for the capture of longhorned beetles (Coleoptera: Cerambycidae) from the subfamilies Lamiinae and Cerambycinae. PLoS ONE 9: e93203.

Aukema J. E., D. G. McCullough, B. Von Holle, A. M. Liebhold, K. Britton, and S. J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. Bioscience 60: 886–897.

Barbour, J. D, J. G. Millar, J. Rodstein, A. M. Ray, D. G. Alston, M. Rejzek, J. D. Dutcher, and L. M. Hanks. 2011. Synthetic 3,5-dimethyldodecanoic acid serves as a general attractant for multiple species of Prionus (Coleoptera: Cerambycidae). Ann. Entomol. Soc. Am. 104: 588–593.

Brockerhoff, E. G., A. M. Liebhold, and H. Jactel. 2006. The ecology of forest insect invasions and advances in their management. Can. J. For. Res. 36: 263–268.

Campbell, F. T. 2001. The science of risk assessment for phytosanitary regulation and the impact of changing trade regulations. BioScience. 51: 148–153.

Chénier, J. V. R., and B. J. R. Philogène 1989. Evaluation of three trap designs for the capture of conifer-feeding beetles and other forest Coleoptera. Can. Entomol. 121: 159–167.

Czokajlo, D., J. McLaughlin, L. I. Abu Ayyash, S. Teale, J. Wickham, J. Warren, R. Hoffman, B. Aukema, K. Raffa, and P. Kirsch. 2003. Intercept™ panel trap (INT PT) effective in management of forest Coleoptera, pp. 125–126. *In* M. L. McManus and A. M. Liebhold (eds.), Proceedings: Ecology, survey and management of forest insects. USDA For. Serv., Northeastern Res. Stn., Gen. Tech. Rep. 311, Newton Square, PA.

Dobesberger, E. J. 2004. *Xylotrechus rufilius*. Pest fact sheet. Plant Health Risk Assessment Unit., Science Division. Canadian Food Inspection Agency.

Fonseca M. G., D. M. Vidal, and P. H. G. Zarbin. 2010. Male-produced sex pheromone of the cerambycid beetle *Hedypathes betulinus*: chemical identification and biological activity. J. Chem. Ecol. 36: 1132–1139.

Ginzel, M. D., and L. M. Hanks. 2005. Role of host plant volatiles in mate location for three species of longhorned beetles. J. Chem. Ecol. 31: 213–217.

Graham, E. E., R. F. Mitchell, P. F. Reagel, J. D. Barbour, J. G. Millar, and L. M. Hanks. 2010. Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles. J. Econ. Entomol. 103: 641–647.

Graham, E. E., and T. M. Poland. 2012. Efficacy of fluon conditioning for capturing cerambycid beetles in different trap designs and persistence on panel traps over time. J. Econ. Entomol. 105: 395–401.

Haack, R. A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. 36: 269–288.

Haack R. A., F. Hérard, J. Sun, and J. J. Turgeon. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: A worldwide perspective. Ann. Rev. Entomol. 55: 521–546.

Hanks, L. M., J. G. Millar, and T. D. Paine. 1996. Mating behavior of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) and the adaptive significance of long "horns". J. Insect Behav. 9: 383–393.

Hanks, L. M., J. G. Millar, J. A. Mongold-Diers, J.C.H. Wong, L. R. Meier, P. F. Reagel, and R. F. Mitchell. 2012. Using blends of cerambycid beetle pheromones and host plant volatiles

to simultaneously attract a diversity of cerambycid species. Can. J. For. Res. 42: 1050–1059.

Lacey, E. S., M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2004. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus acuminatus acuminatus*. J. Chem. Ecol. 30: 1493–1507.

Lacey, E. S., J. A. Moreira, J. G. Millar, A. M. Ray, and L. M. Hanks. 2007. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus mucronatus mucronatus*. Entomol. Exp. Appl. 122: 171–179.

Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. 115: 299–302.

Lingafelter S. W. 2007. Illustrated key to the longhorned wood-boring beetles of the eastern United States. Coleopterists Society, North Potomac, MD.

Linsley, E. G. 1959. Ecology of Cerambycidae. Annu. Rev. Entomol. 4: 99–138.

Linsley, E. G., and J. O. Martin. 1933. Notes on some longicorns from subtropical Texas (Coleop.: Cerambycidae). Entomol. News 44: 178–183.

Linsley, E. G., and J. A. Chemsak. 1997. The Cerambycidae of North America. Part VIII. Bibliography, Index, and Host Plant Index. University of California Press, Berkeley, CA.

Meier, L. R., Y. Zou, J. G. Millar, J. A. Mongold-Diers, and L. M. Hanks. 2016. Synergism between enantiomers creates species-specific pheromone blends and minimizes cross-attraction for two species of cerambycid beetles. J. Chem. Ecol. (in press).

Millar J. G., L. M. Hanks, J. A. Moriera, J. D. Barbour, and E. S. Lacey. 2009. Pheromone chemistry of cerambycid beetles. Chemical Ecology of Wood-Boring Insects (eds. K

Nakamuta and JG Millar), pp. 52–79. Forestry and Forest Products Research Institute, Ibaraki, Japan.

Millar J. G., and L. M. Hanks. 2016. Chemical ecology of cerambycid beetles. *In* Q. Wang (ed.) Cerambycidae of the world: biology and pest management. CRC Press/Taylor & Francis, Boca Raton, FL (in press).

Miller, D. R., and C. M. Crowe. 2011. Relative performance of Lindgren multiple-funnel, intercept panel, and Colossus pipe traps in catching Cerambycidae and associated species in the southeastern United States. J. Econ. Entomol. 104: 1934–1941.

Mitchell R. F., E. E. Graham, J.C.H. Wong, P. F. Reagel, B. L. Striman, G. P. Hughes, M. A. Paschen, M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2011. Fuscumol and fuscumol acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. Entomol. Exp. Appl. 141: 71–77.

National Agricultural Pest Information System. 2013. Survey status of velvet longhorned beetle – *Trichoferus campestris* (2010 to present) [online]. Available from http://pest.ceris.purdue.edu/map.php?code5INALQPA&year53year [accessed 16 June 2016].

Pajares, J. A., G. Álvarez, F. Ibeas, D. Gallego, D. R. Hall, and D. I. Farman. 2010. Identification and field activity of a male-produced aggregation pheromone in the pine sawyer beetle, *Monochamus galloprovincialis*. J. Chem. Ecol. 36: 570–583.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52: 273–288.

Ray, A. M., E. S. Lacey, and L. M. Hanks. 2006. Predicted taxonomic patterns in pheromone production by longhorned beetles. Naturwissenschaften 93: 543–550.

Reddy, G.V.P. 2007. Improved semiochemical-based trapping method for old-house borer, Hylotrupes bajulus (Coleoptera: Cerambycidae). Environ. Entomol. 36: 281–286.

Rodstein, J., J. S. McElfresh, J. D. Barbour, A. M. Ray, L. M. Hanks, and J. G. Millar. 2009. Identification and synthesis of a female-produced sex pheromone for the cerambycid beetle Prionus californicus. J. Chem. Ecol. 35: 590–600.

Ryall K., P. J. Silk, R. P. Webster, J. M. Gutowski, Q. Meng, Y. Li, W. Gao, J. Fidgen, T. Kimoto, T. Scarr, V. Mastro, and J. D. Sweeney. 2014. Further evidence that monochamol is attractive to Monochamus (Coleoptera: Cerambycidae) species, with attraction synergised by host plant volatiles and bark beetle (Coleoptera: Curculionidae) pheromones. Can. Entomol. 147: 564–579.

Sakai, T., Y. Nakagawa, J. Takahashi, K. Iwabuchi, and K. Ishii. 1984. Isolation and identification of the male sex pheromone of the grape borer *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae). Chem. Lett. 13: 263–264.

Silk, P. J., J. Sweeney, J. Wu, J. Price, J.M. Gutowski, and E. G. Kettela. 2007. Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). Naturwissenschaften 94: 697–701.

Slipinski, S. A., R.A.B. Leschen, and J. F. Lawrence. 2011. Order Coleoptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 203–208.

Solomon, J. D. 1995. Agriculture Handbook 706: guide to insect borers of North American broadleaf trees and shrubs. USDA Forest Service, Washington, DC.

Stewart, P. A., and J. J. Lam, Jr. 1970. Capture of forest insects in traps equipped with blacklight lamps. J. Econ. Entomol. 63: 871–873.

Švácha, P., and J. F. Lawrence. 2014. Chapter 2.4 Cerambycidae Latreille, 1802, pp. 77–177. In R.A.B. Leschen and R. G. Beutel (eds.) Handbook of zoology: Arthropoda: Insecta: Coleoptera, beetles. Vol. 3: Morphology and systematics (Phytophaga). Walter de Gruyter, Berlin/Boston.

Sweeney J. D., P. De Groot, L. MacDonald, S. Smith, C. Cocquempot, M. Kenis, and J. M. Gutowski. 2004. Host volatile attractants and traps for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* L., and other longhorned beetles (Coleoptera: Cerambycidae). Environ. Entomol. 33: 844–854.

Sweeney, J. D., P. J. Silk, J. M. Gutowski, J. Wu, M. A. Lemay, P. D. Mayo, and D. I. Magee. 2010. Effect of chirality, release rate, and host volatiles on response of *Tetropium fuscum* (F.), *Tetropium cinnamopterum* Kirby, and *Tetropium castaneum* (L.) to the aggregation pheromone, fuscumol. J. Chem. Ecol. 36: 1309–1321.

Teale, S. A., J. D. Wickham, F. Zhang, J. Su, Y. Chen, W. Xiao, L. M. Hanks, and J. G. Millar. 2011. A male-produced aggregation pheromone of *Monochamus alternatus* (Coleoptera: Cerambycidae), a major vector of pine wood nematode. J. Econ. Entomol. 104: 1592–1598.

Wong, J.C.H., R. F. Mitchell, B. L. Striman, J. G. Millar, and L. M. Hanks. 2012. Blending synthetic pheromones of cerambycid beetles to develop trap lures that simultaneously attract multiple species. J. Econ. Entomol. 105: 906–915.

Yanega D. 1996. Manual 6, field guide to northeastern longhorned beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey, Champaign, IL.

CHAPTER 2: AUTHENTICATED RECORDS OF HOST PLANT ASSOCIATIONS FOR NORTH AMERICAN CERAMBYCID BEETLES

Abstract

Host associations of cerambycid beetles as reported in the secondary literature often are based on a variety of sources, such as accession records of museum specimens and data from field collection of adult beetles, and informal rearing of adult beetles from larval hosts. As a result, host ranges may be incomplete and inaccurate, and the polyphagous nature of the species may be greatly exaggerated. Here, we draw from the primary literature data on host associations of cerambycid species of North America based on 37 published studies in which the taxonomy of host plants were reported, as an authoritative assessment of host range. Larval host associations are presented for 500 species in 64 tribes of seven subfamilies of the Cerambycidae, and one species in the closely related Disteniidae, including 156 genera of host plants in 57 families.

Introduction

Because larvae of cerambycid beetles feed within plants, and do not emerge until they reach adulthood (Švácha and Lawrence 2014), it often is difficult to document the host associations of larvae. Host range as reported in the secondary literature, for example, field guidebooks or faunistic surveys, is usually based on a variety of sources, such as collection records of museum specimens, data from field collection of adult beetles, and informal rearing of adult beetles from larval hosts (e.g., volumes indexed in Linsley and Chemsak 1997). Thus, the accuracy of these data depends on the taxonomic expertise of many contributors whose qualifications are not known. Published host records often are admittedly incomplete and

uncertain, especially when based in part on earlier secondary literature, and scanty information on natural history (e.g., Yanega 1996, Lingafelter 2007). Contributing to the problem are the inevitable changes in the taxonomy of cerambycids and their host plants, and the resulting taxonomic confusion.

Here, I draw from the primary literature data on host associations of cerambycid species that are native to North America based on published studies in which the taxonomy of host plants was reported, as an authoritative assessment of host range. Much of the data comes from field entomologists who have published a wealth of valuable biological information on a diversity of species, notably a number of articles published by E. F. Giesbert, F. T. Hovore, T. C. MacRae, R. L. Penrose, M. E. Rice, and J. E. Wappes. Host associations were derived from rearing adult beetles from larval hosts, or dissecting from hosts plants the larvae, pupae, or adults. The taxonomy of cerambycids, and their host plants, has been verified and updated as needed (see Methods). Although the host associations presented here are undoubtedly incomplete, comprising only a fraction of the cerambycid species that are native to North America, and are an incomplete representation of host plant species for any particular beetle species, they are intended to provide an initial database that can be amended as more information becomes available. The data were summarized so as to assess the diversity of cerambycid species that were known to develop in plant species of particular families, and the diversity of plant species known to be hosts of particular cerambycid species.

Materials and Methods

Information on host associations of North American cerambycid beetles were drawn from 37 articles that were published over the past 110 years. These papers were selected from a

collection of publications (58) that are surveys, records, and notes of cerambycids in North America over the past century plus (1880 - 2014). The criteria for selection out of the 58 were the inclusion of information based on rearing or emergence of adult cerambycids out of woody materials and extraction of pupae and teneral adults. Most of the research was conducted in various regions of the contiguous United States, with three studies in Canada (Table 2.1). The authors of the referenced papers differed as to the goals of their research, some hoping to garner specimens for personal collections, others targeting species that are pests, and still others conducting faunal surveys.

Scientific names for plants were confirmed, and updated if necessary, using the Integrated Taxonomic Information System of the United States government (ITIS 2016). Taxonomy of cerambycids follows Barsevskis (2016).

Results

Cerambycid beetles had been reared, or extracted, from 362 species of plants that represented 156 genera of 57 families of 29 orders (Table 2.2). There were authenticated host records for 500 species of cerambycids, of 64 tribes in seven subfamilies, including one species in the closely related Disteniidae (Table 2.3). The vast majority of these species are native to North America. Among the top five best represented plant families (Fig. 2.1), the Fagaceae had the greatest number of its species recorded as hosts, followed by the Fabaceae and Pinaceae. These families also were among those that had the greatest number of beetle species per plant species, along with the Juglandaceae and Betulaceae (Fig. 2.1). It follows that the same families comprise the individual species that were hosts for the greatest number of beetle species (Table 2.2), among them *Pinus virginiana* Mill. and *Pinus strobus* L. (Pinaceae; 30 and 18 beetle

species, respectively), *Quercus velutina* Lam. (Fagaceae; 21 beetle species), *Carya glabra* (Mill.) Sweet (Juglandaceae; 21 beetle species), and *Leucaena pulverulenta* (Schitdl.) Benth. (Fabaceae; 20 beetle species). Among the remaining plant families (i.e., those not among the top ten families in Fig. 2.1), species in the Cannabaceae were hosts for the greatest number of beetle species on average, with 8.4 ± 2.7 beetle species per plant species.

The cerambycid species associated with the greatest number of plant families were the cerambycines *Euderces pini* (Olivier) (15 plant families), *Elaphidion mucronatum* (Say) (14 families), and *Neoclytus acuminatus acuminatus* (F.) (12 families), and the lamiine *Urgleptes querci* (Fitch) (13). These four species also ranked as the most polyphagous in terms of the number of plant genera with which they were associated, with *U. querci*, *E. mucronatum, E. pini*, and *N. a. acuminatus* having 18, 17, 18, and 15 genera of hosts (Table 2.2). Larvae of all four species develop in dead and dying hosts (Linsley 1963, Gosling 1973, Vlasak 2014), which is consistent with earlier observations that cerambycid species that develop in such hosts tend to be more polyphagous than species that develop in living hosts (Linsley 1959).

Discussion

Of the families represented in Figure 2.1, three of the families were better represented, 72% of the 18 species in Juglandaceae, 48% of the 65 species in Pinaceae, and 40% of the 99 species in Fagaceae were surveyed and included in the literature cited (Kartesz 2015). While Fabaceae, Rosaceae, and Asteraceae were the least well represented, with less than 5% of the species in the family represented here; the reason these three are the least represented families is likely due to the fact that they have more species that are less woody, with a number of herbaceous plant species, therefore not surveyed as extensively since most cerambycids attack

more woody plants. In addition, knowing the average number of species of cerambycid a plant family can support is valuable in management of forests, particularly in determining which tree species may be more important in a particular ecosystem.

Since none of the literature cited had the intent to survey all of the woody plant species in a study area to characterize fully the host associations of the entire cerambycid community, the data presented here cannot be used to assess the host ranges of any cerambycid species, nor be used to compare host ranges of different species. While the ultimate goal of knowing all the host plants a larva of a cerambycid species can develop in may never be achieved for a number of species of cerambycids, having a general taxonomic range of hosts that are suitable is still useful for management of forest ecosystems. The information gathered in this chapter is also useful in future studies regarding host searching and determination of cerambycid beetles, as it can be used for confirm host species and to select a plant or tree species that is out of a species' currently known taxonomic range as a non-host.

References

Barr, W. F., and R. L. Penrose. 1969. Notes on the distribution and bionomics of some Idaho Cerambycidae (Coleoptera). Great Basin Nat. 29: 88–95.

Barsevskis, A. (ed.) 2016. Cerambycidae of the world. http://cerambycidae.org/ (last accessed 8 June 2016).

Beutenmuller, W. 1896. Food-habits of North American Cerambycidae. J. N. Y. Entomol. Soc. 4: 73–81.

Blodgett, S, M. A. Ivie, and M. Majerus. 2005. First larval host record for *Megacyllene angulifera* (Casey) (Cerambycidae). Coleop. Bull. 59: 258–259.

Champlain, A. B., H. B. Kirk, and J. N. Knull. 1925. Notes on Cerambycidae (Coleoptera). Entomol. News 36: 105–109.

Cope, J. 1984. Notes on the ecology of western Cerambycidae. Coleop. Bull., 38: 27–36.

Fattig, P. W. 1947. The Cerambycidae or long-horned beetles of Georgia. Emory Univ. Mus. Bull. 5: 1–48.

Gardiner, L. M. 1957. Deterioration of fire-killed pine in Ontario and the causal wood-boring beetles. Can. Entomol. 89: 241–263.

Gardiner, L. M. 1960. Descriptions of immature forms and biology of *Xylotrechus colonus* (Fab.) (Coleoptera: Cerambycidae). Can. Entomol. 92: 820–825.

Gosling, D.C.L. 1973. An annotated list of the Cerambycidae of Michigan (Coleoptera) part I, introduction and the subfamilies Parandrinae, Prioninae, Spondylinae, Aseminae, and Cerambycinae. Gt. Lakes Entomol. 6: 65–84.

Gosling, D.C.L. 1984. Cerambycid host plants in a southwestern Michigan woodland (Coleoptera: Cerambycidae). Gt. Lakes Entomol. 17: 69–78.

Gosling, D.C.L. 1986. Ecology of the Cerambycidae(Coleoptera) of the Huron Mountains in northern Michigan. Gt Lakes Entomol. 19: 153–162.

Hardy, G. A., and W.H.A. Preece. 1927. Additional notes on some Cerambycidae from Vancouver Island, BC. Pan-Pac. Entomol. 4: 61–67.

Hovore, F. T., and E. F. Giesbert. 1976. Notes on the ecology and distribution of western Cerambycidae (Coleoptera). Coleop. Bull. 30: 349–360.

Hovore, F. T., and R. L. Penrose. 1982. Notes on Cerambycidae co-inhabiting girdles of *Oncideres pustulata* LeConte (Coleoptera: Cerambycidae). Southwest. Nat. 27: 23–27.

Hovore, F. T., R. L. Penrose, and E. F. Giesbert. 1978. Notes on North American Cerambycidae (Coleoptera). Entomol. News 89: 95–100.

Integrated Taxonomic Information System (ITIS). 2015. http://www.itis.gov (last accessed 8 June 2016).

Kartesz, J. T. 2015. The Biota of North America Program (BONAP). North American Plant Atlas. Chapel Hill, N.C. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP). http://bonap.net/napa (last accessed 23 June 2016).

Knull, J. N. 1937. Notes on Coleoptera with descriptions of new species (Buprestidae and Cerambycidae). Entomol. News 48: 36–42.

Lingafelter, S. W. 2007. Illustrated key to the longhorned wood-boring beetles of the eastern United States, Special Publication No. 3. Coleopterists Society, North Potomac, MD.

Linsley, E. G. 1959. Ecology of Cerambycidae. Annu. Rev. Entomol.. 4: 99–138.

Linsley, E. G. 1963. The Cerambycidae of North America. Part IV: Taxonomy and classification of the subfamily Cerambycinae, tribes Elaphidionini through Rhinotragini. Univ. Calif. Press, Berkeley, CA.

Linsley, E. G., and J. A. Chemsak. 1997. The Cerambycidae of North America, part VIII: bibliography, index, and host plant index. Univ. Calif. Press, Berkeley, CA.

Linsley, E. G., and J. O. Martin. 1933. Notes on some longicorns from subtropical Texas (Coleop.: Cerambycidae). Entomol. News 44: 178–183.

Linsley, E. G., J. N. Knull, and M. Statham. 1961. A list of Cerambycidae from the Chiricahua Mountain area, Cochise County, Arizona (Coleoptera). Am. Mus. of Nat. Hist. 1–34.

MacRae, T. C., and M. E. Rice. 2007. Biological and distributional observations on North American Cerambycidae (Coleoptera). Coleop. Bull. 61: 227–263.

Maier, C. T. 2008. Emergence, trapping, and seasonal abundance of adult Cerambycidae (Coleoptera) associated with Cupressaceae in Connecticut. J. Econ. Entomol. 101: 430–437.

Morris, R. F. II. 2002. Distribution and biological notes for some Cerambycidae (Coleoptera) occurring in the southern United States. Insecta Mundi 16: 209–213.

Penrose, R. L., and R. L. Westcott. 1974. Notes on the distribution, hosts and bionomics of some Pacific Northwest Cerambycidae (Coleoptera). Coleop. Bull. 28: 233–236.

Perry, R. H. 1975. Notes on the long-horned beetles of Virginia. III. (Coleoptera: Cerambycidae). Coleop. Bull. 29: 59.

Rice, M. E. 1981. Notes on Cerambycidae from Missouri. Coleop. Bull. 35: 459–462.

Rice, M. E. 1985. New host associations for Cerambycidae (Coleoptera) from selected species of Leguminosae and Rutaceae. J. N. Y. Entomol. Soc. 93: 1223–1225.

Rice, M. E., and W. R. Enns. 1981. The longhorn beetle subfamily Lamiinae (Coleoptera: Cerambycidae) in Missouri. Trans. Miss. Acad. Sci. 15: 89–109.

Rice, M. E., R. H. Turnbow Jr., and F. T. Hovore. 1985. Biological and distributional observations on Cerambycidae from the southwestern United States (Coleoptera). Coleop. Bull. 39: 18–24.

Rogers, C. E. 1977. Bionomics of *Oncideres cingulata* (Coleoptera: Cerambycidae) on mesquite. J. Kans. Entomol. Soc. 50: 222–228.

Schwitzgebel, R. B., and D. A. Wilbur. 1942. Coleoptera associated with ironweed, *Vernonia interior* Small in Kansas. J. Kans. Entomol. Soc. 15: 37–44.

Švácha, P., and J. F. Lawrence. 2014. Chapter 2.4 Cerambycidae Latreille, 1802, pp. 77-177. *In* R.A.B. Leschen and R. G. Beutel (eds.) Handbook of zoology: Arthropoda: Insecta: Coleoptera, beetles. Vol. 3: Morphology and systematics (Phytophaga). Walter de Gruyter, Berlin/Boston.

Swift, I. 2008. Ecological and biogeographical observations of Cerambycidae (Coleoptera) from California, USA. Insecta Mundi 26: 1–7.

Thomas, M. C. 1977. New host records and behavior observations on Florida Cerambycidae. Coleop. Bull. 31: 83–86.

Turnbow, R. H. Jr., and F. T. Hovore. 1979. Notes on Cerambycidae from the southeastern US (Coleoptera). Entomol. News 90: 219–229.

Turnbow, R. H. Jr., and J. E. Wappes. 1978. Notes on Texas Cerambycidae (Coleoptera). Coleop. Bull. 32: 367–372.

Tyson, W. H. 1966. Notes on reared Cerambycidae. Pan-Pac. Entomol. 42: 201.

Tyson, W. H. 1970. Cerambycidae of the Panamint Mountains, California (Coleoptera). Pan-Pac. Entomol. 46: 296–299.

Vlasak, J. 2014. New larval host records for North American Cerambycidae (Coleoptera). Coleop. Bull. 68: 316–320.

Vlasak, J., and K. Vlasakova. 2002. Records of Cerambycidae (Coleoptera) in Massachusetts with notes on larval hosts. Coleop. Bull. 56: 203–219.

Vogt, G. B. 1949. Notes on Cerambycidae from the lower Rio Grande valley, Texas. Pan-Pac. Entomol. 25: 137–144.

Webster, F. W. 1897. Notes on various species of Coleoptera. J. N. Y. Entomol. Soc. 5: 201–205.

Yanega, D. 1996. Field guide to northeastern longhorned beetles (Coleoptera: Cerambycidae), Manual 6. Illinois Natural History Survey, Champaign, IL.

Tables

Table 2.1. Publications that were the sources of data on host plant associations of North American cerambycid beetles, and the method used to identify beetle species.

Geographical region	Reference	Primary source of specimens	Method
United States			
Midwest[a]	Gosling 1984, 1986	Field collection	Rearing adults
	Rice 1981	Field collection	Rearing adults
	Rice and Enns 1981	Field collection	Rearing adults
	Schwitzgebel and Wilbur 1942	Field collection	Rearing adults
	Webster 1897	Field collection	Larval gallery
Northeast[b]	Champlain et al. 1925	Field rearing	Rearing adults
	Maier 2008	Field collection	Rearing adults
	Penrose and Westcott 1974	Field collection	Rearing adults
	Vlasak and Vlasakova 2002	Field collection	Rearing adults
Southeast[c]	Fattig 1947	Field collection	Rearing adults
	Morris 2002	Field collection	Rearing adults
	Perry 1975	Field collection	Rearing adults
	Thomas 1977	Field collection	Rearing adults
	Turnbow and Hovore 1979	Field collection	Rearing adults
Southwest[d]	Hovore and Penrose 1982	Field collection	Rearing adults
	Linsley and Martin 1933	Field collection	Rearing adults
	Linsley et al. 1961	Field collection	Rearing adults
	Rice 1985	Field collection	Rearing adults
	Rice et al. 1985	Field collection	Rearing adults
	Rogers 1977	Field collection	Rearing adults
	Turnbow and Wappes 1978	Field collection	Rearing adults

Table 2.1 (cont.).

Geographical region	Reference	Primary source of specimens	Method
	Vogt 1949	Field collection	Rearing adults, field dissection of pupae and teneral adults from hosts
West[e]	Barr and Penrose 1969	Field collection	Rearing adults
	Blodgett et al. 2005	Field collection	Rearing, collection of pupae
	Hovore and Giesbert 1976	Field collection	Rearing, dissection of adults from pupal cells
	Swift 2008	Field collection	Rearing adults
	Tyson 1966	Field rearing	Rearing adults
	Tyson 1970	Field collection	Rearing adults
Multiple regions			
"North America"	Beutenmuller 1896	Field collection	Rearing adults
"North America"	MacRae and Rice 2007	Field collection	Rearing adults
West and Southwest	Cope 1984	Field collection	Rearing adults
Southeast and Southwest	Hovore et al. 1978	Field collection	Rearing adults
	Knull 1937	Field collection	Rearing adults, dissection of adults from pupal cells
Canada			
British Columbia	Hardy and Preece 1927	Field collection	Rearing adults
Ontario	Gardiner 1957	Field collection	Rearing adults
Quebec	Gardiner 1960	Field collection	Rearing adults

[a] Midwest = ND, SD, NE, KS, MN, IA, MO, WI, IL, MI, IN, OH

[b] Northeast = ME, NH, VT, MA, RI, CT, NY, PA, NJ, DE, MD

Table 2.1 (cont.).

[e] Southeast = KY, WV, VA, TN, NC, AR, LA, MS, AL, GA, SC, FL

[d] Southwest = AZ, NM, OK, TX

[e] West = WA, OR, CA, ID, MT, WY, CO, UT, NV

Table 2.2. North American plant species from which cerambycid beetles have been obtained, the code for the plant taxa (numerically assigned as ordered in table), and the number of cerambycid species which were associated with that plant species.

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
Apiales			
Apiaceae	*Lomatium lucidum* (Nutt. ex Torr. & A. Gray) Jeps.	1	1
	L. utriculatum (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose	2	1
Aquifoliales			
Aquifoliacae	*Ilex* sp. L.	3	1
Arecales			
Arecaceae	*Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f.	4	1
Asparagales			
Asparagaceae	*Agave* lechuguilla Torr.	5	1
	Dasylirion sp. Zucc.	6	1
	Hesperoyucca whipplei (Torr.) Baker	7	1
	Yucca sp. L.	8	1
	Y. brevifolia Engelm	9	1
	Y. treculeana Carrière	10	1
Asterales			
Asteraceae	*Ambrosia* sp. L.	11	2
	A. artemisiifolia L.	12	1
	A. psilostachya DC.	13	1
	A. trifida L.	14	1
	Artemisia tridentata Nutt.	15	2

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	Aster sp. L.	16	1
	Baccharis angustifolia Michx.	17	2
	B. halimifolia L.	18	3
	B. neglecta Britton	19	1
	Chrysothamnus viscidiflorus (Hook.) Nutt.	20	1
	Eurybia macrophylla (L.) Cass.	21	1
	Encelia farinosa A. Gray ex Torr.	22	1
	Euthamia graminifolia (L.) Nutt.	23	1
	Gutierrezia sarothrae (Pursh) Britton & Rusby	24	1
	Helianthus sp. L.	25	1
	Silphium terebinthinaceum Jacq.	26	1
	Solidago caesia L.	27	1
	S. gigantea Aiton	28	1
	S. juncea Aiton	29	1
	Vernonia baldwinii Torr.	30	4
	Xanthium sp. L.	31	1
Caryophyllales			
Amaranthaceae	*Atriplex canescens* var. *canescens* (Pursh) Nutt.	32	1
	A. confertifolia (Torr. & Frém.) S. Watson	33	1
Cactaceae	*Cylindropuntia acanthocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth	34	1
	Echinocactus texensis Hopffer	35	1
	Opuntia engelmannii var. *lindheimeri* (Engelm.) B.D. Parfitt & Pinkava	36	1
Sarcobataceae	*Sarcobatus vermiculatus* (Hook.) Torr.	37	2

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
Celastrales			
Celastraceae	*Celastrus orbiculatus* Thunb.	38	2
	Euonymus sp. L.	39	2
Cornales			
Cornaceae	*Cornus* sp. L.	40	11
	C. alternifolia L. f.	41	1
	C. amomum Mill.	42	1
	C. florida L.	43	6
	Nyssa sp. L.	44	3
	N. sylvatica Marshall	45	3
Crossosomatales			
Staphyleaceae	*Staphylea trifolia* L.	46	3
Dipsacales			
Adoxaceae	*Sambucus nigra* ssp. *canadensis* (L.)	47	1
	S. racemosa var. *racemosa* L.	48	1
	Viburnum sp. L.	49	1
	V. acerifolium L.	50	1
	V. dentatum L.	51	3
Ericales			
Ebenaceae	*Diospyros* sp. L.	52	3
	D. virginiana L.	53	6
Ericaceae	*Arctostaphylos patula* Greene	54	1
	A. pungens Kunth	55	1
	Rhododendron L. (Azaleas)	56	2
Sapotaceae	*Sideroxylon foetidissimum* Jacq.	57	4
	S. lanuginosum Michx.	58	2
	S. tenax L.	59	1

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
Fabales			
Fabaceae	*Acacia* sp. Mill.	60	3
	A. angustissima (Mill.) Kuntze	61	1
	Amorpha sp. Hübner	62	1
	Cercis sp. L.	63	7
	C. canadensis L.	64	14
	Coursetia microphylla A. Gray	65	2
	Dalea candida Michx. ex Willd.	66	1
	D. formosa Torr.	67	2
	Ebenopsis ebano (Berland.) Barneby & J.W. Grimes	68	9
	Eysenhardtia polystachya (Ortega) Sarg.	69	2
	E. texana Scheele	70	2
	Gleditsia triacanthos L.	71	6
	Glycine max (L.) Merr.	72	1
	Gymnocladus dioicus (L.) K. Koch	73	2
	Havardia pallens (Benth.) Britton & Rose	74	6
	Leucaena pulverulenta (Schitdl.) Benth.	75	20
	Lysiloma latisiliquum (L.) Benth.	76	8
	Mimosa aculeaticarpa Ortega	77	1
	M. aculeaticarpa var. *biuncifera* (Benth.) Barneby	78	1
	M. dysocarpa Benth.	79	1
	Olneya tesota A. Gray	80	1
	Parkinsonia sp. L.	81	2
	P. aculeata L.	82	6
	P. florida (Benth. ex A. Gray) S. Watson	83	1
	P. texana var. *texana* (A. Gray) S. Watson	84	1

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	Piscidia piscipula (L.) Sarg.	85	5
	Pithecellobium sp. Mart.	86	1
	Prosopis sp. L.	87	10
	P. glandulosa Torr.	88	14
	P. juliflora (Sw.) DC.	89	3
	P. pubescens Benth.	90	1
	Psorothamnus fremontii var. *fremontii* (Torr. ex A. Gray) Barneby	91	2
	Robinia sp. L.	92	1
	R. pseudoacacia L.	93	3
	Senegalia berlandieri (Benth.) Britton & Rose	94	1
	Senna tora (L.)	95	1
	Sesbania drummondii (Rydb.) Cory	96	10
	Sophora secundiflora (Ortega) Lag. ex DC.	97	5
	Vachellia constricta (Benth.) Seigler & Ebinger	98	2
	V. farnesiana var. *farnesiana* (L.) Wight & Arn.	99	13
	V. rigidula (Benth.) Seigler & Ebinger	100	4
	Wisteria sp. Nutt.	101	2
Fagales			
Betulaceae	*Alnus* sp. Mill.	102	3
	A. rhombifolia Nutt.	103	2
	A. rubra Bong.	104	1
	Betula sp. L.	105	11
	B. alleghaniensis Britton	106	3
	B. nigra L.	107	13

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	Carpinus sp. L.	108	1
	C. caroliniana ssp. *virginiana* (Marshall) Furlow	109	1
	C. caroliniana Walter	110	13
	Ostrya sp. Scop.	111	2
	O. virginiana (Mill.) K. Koch	112	5
Fagaceae	*Castanea* sp. Mill.	113	10
	C. dentata (Marsh.) Borkh.	114	2
	Fagus sp. L.	115	1
	F. grandifolia Ehrh.	116	8
	F. sylvatica L.	117	9
	Lithocarpus densiflorus (Hook. & Arn.) Rehder	118	7
	Quercus sp. L.	119	49
	Quercus sp. L. (red)	120	1
	Quercus sp. L. (white)	121	1
	Q. agrifolia (E.J. Palmer) Stoynoff & W. J. Hess	122	10
	Q. alba L.	123	8
	Q. arizonica Sarg.	124	6
	Q. berberidifolia Liebm.	125	2
	Q. bicolor Willd.	126	3
	Q. chrysolepis Liebm.	127	6
	Q. douglasii Hook. & Arn.	128	4
	Q. dumosa Nutt.	129	2
	Q. emoryi Torr.	130	2
	Q. falcata Mivhx.	131	1
	Q. garryana Douglas ex Hook.	132	2

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	Q. geminata Small	133	3
	Q. grisea Liebm.	134	2
	Q. hypoleucoides A. Camus	135	2
	Q. inopina Ashe	136	6
	Q. john-tuckeri Nixon & C. H. Mull.	137	5
	Q. kelloggii Newberry	138	6
	Q. laevis Walter	139	3
	Q. laurifolia Michx	140	4
	Q. lobata Née	141	4
	Q. lyrata Walter	142	1
	Q. macrocarpa Michx.	143	3
	Q. montana Willd.	144	1
	Q. muhlenbergii Engelm.	145	7
	Q. pagoda Raf.	146	1
	Q. palustris Münchh.	147	4
	Q. phellos L.	148	12
	Q. rubra L.	149	3
	Q. stellata Wangenh.	150	6
	Q. texana Buckley	151	1
	Q. turbinella Greene	152	2
	Q. vaccinifolia Kellogg	153	1
	Q. vaseyana Buckley	154	3
	Q. velutina Lam.	155	21
	Q. virginiana Mill.	156	1
	Q. wislizeni A. DC.	157	7
Juglandaceae	*Carya* sp. Nutt.	158	26
	C. aquatica (F. Michx.) Elliott	159	1
	C. cordiformis (Wangenh.) K. Koch	160	3

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	C. floridana Sarg.	161	4
	C. glabra (Mill.) Sweet	162	21
	C. illinoinensis (Wangenh.) K. Koch	163	12
	C. laciniosa (Michx. f.) G. Don	164	3
	C. ovata (Mill.) K. Koch	165	5
	C. tomentosa (Lam. ex Poir.) Nutt.	166	2
	Juglans sp. L.	167	1
	J. californica S. Watson	168	2
	J. cinerea L.	169	4
	J. major (Torr.) A. Heller	170	2
	J. nigra L.	171	6
	J. regia L.	172	3
Gentianales			
Apocynaceae	*Apocynum cannabinum*	173	1
	Asclepias sp. L.	174	4
Lamiales			
Acanthaceae	*Avicennia germinans* (L.) L.	175	7
Bignoniaceae	*Chilopsis linearis* (Cav.) Sweet	176	1
Lamiaceae	*Collinsonia canadensis* L.	177	1
	Scutellaria sp. L.	178	1
Oleaceae	*Forestiera segregata* (Jacq.) Krug & Urb.	179	1
	F. segregata var. *segregata* (Jacq.) Krug & Urb.	180	1
	Fraxinus sp. L.	181	9
	F. americana L.	182	1
	F. anomala Torr. ex S. Watson	183	1
	F. excelsior L.	184	1
	F. nigra Marsh.	185	1

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	F. quadrangulata Michx.	186	2
Paulowniaceae	*Paulownia tomentosa* (Thunb.) Steud.	187	1
Lauraceae	*Lindera benzoin* (L.) Blume	188	2
	Sassafras sp. Nees & Eberm.	189	1
	S. albidum (Nutt.) Nees	190	1
	Umbellularia californica (Hook. & Arn.) Nutt.	191	1
Magnoliales			
Annonaceae	*Asimina triloba* (L.) Dunal	192	1
Magnoliaceae	*Liriodendron tulipifera* L.	193	7
Malpighiales			
Euphorbiaceae	*Bernardia myricifolia* (Scheele) S. Watson	194	1
	Ricinus communis L.	195	1
Hypercaceae	*Hypericum prolificum* L.	196	1
Rhizophoraceae	*Rhizophora mangle* L.	197	2
Salicaceae	*Populus* sp. L.	198	6
	P. deltoides W. Bartram ex Marshall	199	1
	P. fremontii S. Watson	200	1
	P. tremuloides Michx.	201	1
	Salix sp. L.	202	16
	S. lasiandra Benth.	203	2
	S.nigra Marshall	204	7
	S. thurberi Rowlee	205	5
Malvales			
Malvaceae	*Gossypium* sp. L.	206	2
	Malvaviscus arboreus var. *drummondii* (Torr. & A. Gray) Schery	207	1
	Tilia sp. L.	208	6

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	T. americana L.	209	14
Myrtales			
Combretaceae	*Conocarpus* sp. L.	210	1
	C. erectus L.	211	3
Myrtaceae	*Eucalyptus* sp. L'Hér.	212	1
Pinales			
Cupressaceae	*Callitropsis arizonica* (Greene) D. P. Little	213	1
	C. macrocarpa (Hartw.) D. P. Little	214	2
	Calocedrus decurrens (Torr.) Florin	215	3
	Chamaecyparis thyoides (L.) Britton, Sterns & Poggenb.	216	7
	*Hesperocyparis forbesii (*Jeps.) Bartel	217	2
	Juniperus sp. L.	218	2
	J. ashei J. Buchholz	219	2
	J. californica Carrière	220	1
	J. deppeana Steud.	221	2
	J. occidentalis Hook.	222	1
	J. osteosperma (Torr.) Little	223	2
	J. virginiana L.	224	2
	Sequoia sempervirens (Lamb. ex D. Don) Endl.	225	2
	Taxodium distichum (L.) Rich.	226	6
	Thuja occidentalis L.	227	1
Pinaceae	*Abies* sp. Mill.	228	1
	A. balsamea (L.) Mill.	229	2
	A. bracteata (D. Don) D. Don ex Poit.	230	2
	A. concolor (Gordon & Glend.) Lindl. ex Hildebr.	231	14

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	A. magnifica A. Murray	232	1
	Larix laricina (Du Roi) K. Koch	233	5
	Picea sp. A. Dietr	234	2
	P. abies (L.) Karst.	235	1
	P. glauca (Moench) Voss	236	2
	P. rubens Sarg.	237	1
	Pinus sp. L.	238	17
	Pinus sp.(pinyon pine)	239	1
	P. attenuata Lemmon	240	2
	P. banksiana Lamb.	241	11
	P. cembroides Zucc.	242	4
	P. contorta var. *murrayana* (Balf.) Engelm.	243	1
	P. coulteri D. Don	244	2
	P. edulis Engelm.	245	1
	P. flexilis E. James	246	1
	P. jeffreyi Balf.	247	2
	P. leiophylla var. *chihuahuana* (Engelm.) Shaw	248	1
	P. monophylla Torr. & Frém.	249	8
	P. monticola Douglas ex D. Don	250	1
	P. ponderosa Douglas ex P. Lawson & C. Lawson	251	2
	P. radiata D. Don	252	2
	P. resinosa Aiton	253	10
	P. rigida Mill.	254	7
	P. sabiniana Douglas ex Douglas	255	9
	P. strobus L.	256	18
	P. virginiana Mill.	257	30

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	Pseudotsuga sp. Carrière	258	1
	P. macrocarpa (Vasey) Mayr	259	2
	P. menziesii (Mirb.) Franco	260	8
	P. menziesii var. *menziesii* (Mirb.) Franco	261	9
	Tsuga sp. Carrière	262	1
	T. canadensis (L.) Carrière	263	5
Proteales			
Platanaceae	*Platanus occidentalis* L.	264	2
Ranunculales			
Berberidaceae	*Berberis harrisoniana* Kearney & Peebles	265	3
Ranunculaceae	*Anemone virginiana* L.	266	1
Rosales			
Cannabaceae	*Celtis* sp. L.	267	8
	C. laevigata Willd.	268	11
	C. lindheimeri Englem. ex K. Koch	269	9
	C. occidentalis L.	270	5
	C. pallida Torr.	271	5
	C. reticulata Torr.	272	12
	C. tenuifolia Nutt.	273	9
Moraceae	*Ficus* sp. L.	274	6
	F. aurea Nutt.	275	4
	Maclura pomifera (Raf.) C. K. Schneid.	276	2
	Morus sp. L.	277	5
	M. alba L.	278	1
	M. microphylla Buckley	279	2
	M. rubra L.	280	1
Rhamnaceae	*Condalia* sp. Cav.	281	2
	C. cordulatus Kellogg	282	1

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	C. crassifolius Torr.	283	1
	C. integerrimus Hook. & Arn.	284	2
	C. spinosus Nutt.	285	2
	C. globosa var. *pubescens* I.M. Johnst.	286	1
	Rhamnus californica Eschsch	287	3
Rosaceae	*Adenostoma fasciculatum* Hook. & Arn.	288	4
	Amelanchier arborea (F. Michx.) Fernald	289	1
	A. canadensis (L.) Medik.	290	1
	A. utahensis Koehne	291	2
	Cercocarpus betuloides Nutt.	292	5
	C. ledifolius Nutt.	293	1
	C. montanus Raf.	294	2
	Crataegus sp. L.	295	4
	C. crus-galli L.	296	1
	C. viridis L.	297	12
	Heteromeles arbutifolia (Lindl.) M. Roem.	298	1
	Malus sp. Mill.	299	3
	M. pumila Mill.	300	4
	Physocarpus opulifolius (L.) Maxim.	301	1
	Prunus sp. L.	302	1
	P. americana Marshall	303	1
	P. avium (L.) L.	304	2
	P. caroliniana (Mill.) Aiton	305	1
	P. emarginata (Douglas) Eaton	306	1
	P. fremontii S. Watson	307	1
	P. ilicifolia (Nutt. ex Hook. & Arn.) D. Dietr.	308	1
	P. pensylvanica L. f.	309	1

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
	P. persica (L.) Batsch	310	1
	P. serotina Ehrh.	311	7
	Purshia tridentata (Pursh) DC.	312	1
	Pyrus sp. L.	313	1
	Rubus sp. L.	314	1
	Sorbus sp. L.	315	1
Ulmaceae	*Ulmus* sp. L.	316	7
	U. alata Michx.	317	1
	U. americana L.	318	3
	U. crassifolia Nutt.	319	6
	U. parvifolia Jacq.	320	1
	U. procera Salisb.	321	1
	U. rubra Muhl.	322	3
Santalales			
Olacaceae	*Ximenia americana* L.	323	1
Sapindales			
Anacardiaceae	*Metopium toxiferum* (L.) Krug & Urb.	324	12
	Rhus sp. L.	325	3
	R. aromatica Aiton	326	4
	R. copallinum var. *lanceolata* A. Gray	327	1
	R. glabra L.	328	3
	R. integrifolia (Nutt.) Benth. & Hook. f. ex W. H. Brewer & S. Watson	329	1
	R. virens var. *choriophylla* (Wooton & Standl.) L. D. Benson	330	1
	Toxicodendron pubescens Mill.	331	5
	T. radicans (L.) Kuntze	332	9
Burseraceae	*Bursera simaruba* (L.) Sarg.	333	6

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
Rutaceae	*Citrus* sp. L.	334	3
	Ptelea trifoliata ssp. *angustifolia* (Benth.) M. E. Jones	335	1
	Zanthoxylum clava-herculis L.	336	3
	Z. fagara (L.) Sarg.	337	4
Sapindaceae	*Acer* sp. L.	338	14
	A. glabrum Torr.	339	1
	A. grandidentatum Nutt.	340	2
	A. grandidentatum var. *grandidentatum* Nutt.	341	1
	A. macrophyllum Pursh	342	4
	A. negundo L.	343	6
	A. pensylvanicum L.	344	1
	A. rubrum L.	345	18
	A. saccharinum L.	346	1
	A. saccharum Marsh.	347	5
	Aesculus californica (Spach) Nutt.	348	1
	A. glabra Willd.	349	4
	A. pavia L.	350	5
	Dodonaea viscosa (L.) Jacq.	351	1
	Sapindus sp. L.	352	5
	S. saponaria var. *drummondii* (Hook. & Arn.) L. D. Benson	353	2
	Ungnadia speciosa Endl.	354	2
Saxifragales			
Altingiaceae	*Liquidambar* sp. L.	355	1
	L. styraciflua L.	356	3
Grossulariaceae	*Ribes hirtellum* Michx.	357	1

Table 2.2 (cont.).

Order/Family	**Scientific name**	**Plant code**	**# beetle species**
Hamamelidaceae	*Hamamelis virginiana* L.	358	7
Solanales			
Solanaceae	*Lycium cooperi* A. Gray	359	1
Vitales			
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	360	5
	Vitis sp. L.	361	7
	Vitis riparia Michx.	362	4

Table 2.3. Species of cerambycid beetles, the number of plant taxa which are known to be their larval hosts, and the host plant taxa (host plant code as assigned in Table 2.2).

Taxomony	**# plant taxa**	**Host plant code**
Cerambycinae		
Achrysonini		
Achryson jolyi Monné	3	68, 99, 319
A. surinamum (L.)	1	75
Geropa concolor (LeConte)	3	75, 82, 88
Agallissini		
Osmopleura chamaeropis (Horn)	1	4
Anaglyptini		
Cyrtophorus verrucosus (Olivier)	8	52, 63, 64, 110, 115, 162, 257, 295
Tilloclytus geminatus (Haldeman)	12	39, 40, 105, 107, 126, 158, 237, 257, 273, 297, 358, 361
Bothriospilini		
Chrotoma dunniana Casey	1	286
Gnaphalodes trachyderoides Thomson	4	75, 267, 271, 319
Knulliana cincta (Drury)	3	119, 158, 352
K. c. cincta (Drury)	6	53, 87, 143, 147, 148, 150
K. c. sonorensis (Schaeffer)	2	119, 154
K. c. spinifera (F.)	5	76, 163, 211, 275, 324
Callichromatini		
Plinthocoelium suaveolens suaveolens (L.)	1	58
Callidiini		
Callidiellum rufipenne Motschulsky	1	227
C. virescens Chemsak and Linsley	1	214

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Callidium antennatum Newman	1	238
C. a. hesperum Casey	2	239, 242
C. californicum Casey	1	216
C. frigidum Casey	2	217, 224
C. texanum Schaeffer	1	223
C. vancouverensis Van Dyke	1	261
C. vandykei Linsley	2	215, 225
Phymatodes aeneus LeConte	1	261
P. aereus (Newman)	2	111, 113
P. amoenus (Say)	2	361, 362
P. blandus blandus (LeConte)	1	202
P. decussatus (LeConte)	3	118, 128, 157
P. d. australis Chemsak	1	137
P. d. decussatus (LeConte)	2	137, 202
P. infuscatus (LeConte)	1	118
P. juglandis Leng	1	168
P. lecontei Linsley	6	118, 119, 122, 128, 141, 157
P. maculicollis LeConte	2	230, 231
P. nigerrimus Van Dyke	1	260
P. nitidus LeConte	1	216
P. testaceus (L.)	4	149, 162, 231, 257
P. varius (F.)	5	119, 124, 135, 150, 154
P. vilitatis Linsley	1	260
P. vulneratus (LeConte)	2	342, 361
Physocnemum brevilineum (Say)	1	316
Pronocera collaris lecontei (Chemsak)	2	231, 232

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Semanotus amethystinus (LeConte)	1	216
S. juniperi (Fisher)	1	218
S. ligneus amplus Hardy	2	216, 223
Clytini		
Calloides lorquini (Buquet)	2	153, 157
C. nobilis nobilis (Harris)	1	155
Clytoleptus albofasciatus (Laporte and Gory)	2	361, 362
Clytus blaisdelli Van Dyke	2	238, 258
C. chemsaki Hovore & Giesbert	1	259
C. marginicollis Laporte and Gory	2	234, 238
C. planifrons (LeConte)	1	231
C. ruricola (Olivier)	2	116, 158
Megacheuma brevipennis (LeConte)	3	32, 33, 37
Megacyllene angulifera (Casey)	1	66
M. antennata (White)	1	88
M. caryae (Gahan)	4	64, 87, 162, 276
M. robiniae (Forst)	1	93
M. robusta Linsley & Chemsak	1	88
M. snowi (Casey)	1	92
Neoclytus acuminatus (F.)	6	99, 119, 158, 163, 181, 202
N. a. acuminatus (F.)	22	64, 97, 110, 123, 143, 145, 148, 155, 162, 163, 165, 186, 204, 205, 209, 226, 273, 297, 311, 332, 345, 362
N. a. hesperus Linsley	7	17, 86, 88, 100, 119, 271, 334

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
N. augusti (Chevrolat)	5	88, 269, 319, 334, 352
N. balteatus LeConte	2	282, 284
N. caprea (Say)	6	53, 124, 130, 154, 181, 272
N. conjunctus (LeConte)	3	138, 141, 157
N. cordifer (Klug)	7	57, 76, 85, 133, 161, 175, 323
N. irroratus (LeConte)	1	130
N. jouteli jouteli Davis	3	133, 139, 155
N. j. simplarius Blatchley	1	139
N. magnus Schaeffer	1	288
N. mucronatus (F.)	2	158, 319
N. m. mucronatus (F.)	4	53, 163, 257, 268
N. m. vogti Linsley	1	88
N. muricatulus infans Casey	1	252
N. m. muricatulus (Kirby)	1	233
N. nubilus Linsley	1	231
N. resplendens Linsley	1	54
N. scutellaris (Olivier)	5	147, 148, 150, 155, 158
N. senilis (F.)	1	18
N. vanduzeei Van Dyke	1	55
Placosternus difficilis (Chevrolat)	4	87, 88, 99, 100
Sarosesthes fulminans (F.)	4	113, 119, 155, 169
Stenocentrus suturalis (Olivier)	2	57, 324
Triodoclytus lanifer (LeConte)	2	127, 283
Xylotrechus aceris Fisher	3	345, 346, 347

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
X. colonus (F.)	13	40, 107, 110, 145, 147, 149, 150, 155, 162, 205, 257, 263, 299
X. convergens LeConte	1	297
X. insignis Casey	1	202
X. lengi Schaeffer	1	231
X. longitarsis Casey	1	260
X. nauticus (Mannerheim)	9	118, 119, 122, 128, 141, 172, 203, 212, 300
X. quadrimaculatus (Haldeman)	4	102, 105, 110, 116
X. quercus Schaeffer	1	119
X. sagittatus (Germar)	3	238, 241, 256
X. s. chiricahuae Chemsak	1	228
X. s. sagittatus (Germar)	1	257
X. undulatus (Say)	4	233, 241, 256, 261
Compsocerini		
Rosalia funebris Motschulsky	3	320, 340, 343
Curiini		
Curius dentatus Newman	2	161, 338
Dryobiini		
Dryobius sexnotatus Linsley	1	322
Eburiini		
Eburia distincta Haldeman	2	18, 226
E. haldemani LeConte	2	217, 267
E. linsleyi Lacey	1	152
E. mutica LeConte	9	74, 75, 82, 88, 96, 97, 124, 271, 336
E. ovicollis LeConte	1	89

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
E. quadrigeminata (Say)	1	119
E. stigma (Olivier)	4	57, 76, 175, 324
Susuacanga falli (Linsley)	1	81
S. stigmatica (Chevrolat)	1	267
Elaphidiini		
Aneflomorpha lineare (LeConte)	3	129, 288, 312
A. rectilinea rectilinea Casey	1	326
A. subpubescens (LeConte)	1	123
Aneflus levettei (Casey)	1	79
A. prolixus insoletus Chemsak and Linsley	1	94
Anelaphus albofasciatus (Linell)	1	34
A. brevidens (Schaeffer)	1	69
A. cinereus (Olivier)	2	76, 324
A. debilis (LeConte)	6	17, 74, 75, 87, 267, 337
A. inermis (Newman)	4	59, 60, 96, 175
A. inflaticollis Chemsak	2	37, 281
A. moestus moestus (LeConte)	9	88, 97, 100, 119, 171, 242, 269, 272, 326
A. m. pinorum (Casey)	1	140
A. parallelus Newman	13	45, 105, 107, 120, 123, 140, 148, 149, 150, 155, 162, 273, 297
A. piceum (Chemsak)	1	202
A. piceus (Chemsak)	2	22, 98
A. pumilus (Newman)	6	40, 107, 123, 148, 155, 347
A. subdepressum (Schaeffer)	2	272, 351
A. subinermis Linsley	2	5, 6

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
A. tuckeri (Casey)	1	134
A. villosus (F.)	8	45, 64, 162, 209, 257, 263, 332, 345
Anopliomorpha rinconium (Casey)	1	134
Anoplocurius canotiae Fisher	2	265, 279
A. incompletus Linsley	1	88
Astromula nitidum Chemsak & Linsley	1	9
Curtomerus flavus (F.)	1	175
Elaphidion cryptum Linsley	2	197, 324
E. knulli Linsley	1	175
E. linsleyi Knull	4	99, 327, 330, 354
E. mimeticum Schaeffer	1	99
E. mucronatum (Say)	19	53, 71, 96, 101, 110, 116, 119, 135, 158, 181, 204, 226, 235, 272, 292, 311, 332, 338, 345
E. tectum LeConte in Schwarz	1	18
Elaphidionopsis fasciatipennis Linsley	1	272
Enaphalodes atomarius (Drury)	2	119, 155
E. cortiphagus (Craighead)	2	123, 144
E. hispicornis (L.)	1	122
E. niveitectus (Schaeffer)	1	124
E. rufulus (Haldeman)	1	119
E. seminitidus (Horn in Leng)	1	87
Neaneflus brevispinus (LeConte)	1	67
N. fuchsi (Wickham)	1	359
Orwellion gibbulum arizonense (Casey)	1	124
Parelaphidion aspersum (Haldeman)	3	107, 155, 268

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
P. incertum (Newman)	1	158
Pseudoperiboeum lengi (Schaeffer)	1	69
Psyrassa pertenuis (Casey)	1	211
P. unicolor (Randall)	4	117, 119, 158, 171
Stenosphenus debilis Horn	3	62, 200, 279
S. dolosus Horn	5	75, 87, 88, 99, 100
S. lugens LeConte	2	75, 269
S. notatus (Olivier)	3	159, 162, 164
S. sobrius (Newman)	4	87, 267, 272, 291
Stizocera floridana Linsley	1	180
Eumichthini		
Eumichthus oedipus LeConte	1	261
Poecilobrium chalybaeum (LeConte)	1	294
Graciliini		
Hypexilis pallida Horn	1	319
Hesperophanini		
Brothylus conspersus LeConte	3	122, 137, 138
B. gemmulatus LeConte	1	122
Eucrossus villicornis LeConte	2	249, 255
Haplidus laticeps Knull	1	98
H. testaceus LeConte	2	245, 249
Hesperanoplium antennatum (Linsley)	7	127, 291, 293, 298, 308, 329, 339
Hesperophanes pubescens (Haldeman)	1	119
Malobidion brunneum Schaeffer	5	183, 265, 290, 294, 326
Meganoplium imbelle (LeConte)	3	127, 138, 141
Osmidus guttatus LeConte	4	81, 87, 89, 90
Holopleurini		

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Holopleura marginata LeConte	3	230, 259, 260
Hyboderini		
Hybodera debilis LeConte	1	118
H. tuberculata LeConte	1	342
Lampropterus cyanipennis (LeConte)	1	122
L. ruficollis (LeConte)	1	128
Pseudopilema hoppingi (Van Dyke)	1	127
Hylotrupini		
Hylotrupes bajulus (L.)	2	238, 263
Ibidionini		
Heterachthes ebenus Newman	2	136, 238
H. nobilis LeConte	1	87
H. quadrimaculatus Haldeman	3	162, 164, 193
H. sablensis Blatchley	1	175
Neocompsa exclamationis (Thomson)	3	68, 75, 99
N. mexicana (Thomson)	5	19, 68, 75, 99, 269
Lissonotini		
Lissonotus flavocinctus puncticollis Bates	1	99
Methiini		
Methia arizonica Schaeffer	1	80
M. brevis Fall	2	91, 194
M. curvipennis Chemsak & Linsley	1	307
M. mormona Linell	4	170, 202, 221, 265
M. necydalea (F.)	3	148, 156, 269
Styloxus bicolor (Champlain & Knull)	3	213, 218, 221
S. fulleri fulleri (Horn)	1	272
Tessaropa tenuipes (Haldeman)	2	112, 358
Molorchini		

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Molorchus bimaculatus Say	5	40, 105, 111, 158, 338
M. b. bimaculatus Say	4	46, 162, 345, 362
M. b. californicus Linsley	1	285
M. b. celti Knull	1	270
M. b. corni Haldeman	2	133, 328
M. b. semiustus (Newman)	3	163, 297, 361
M. eburneus Linsley	1	231
M. longicollis LeConte	3	231, 260, 261
Obriini		
Obrium maculatum (Olivier)	17	64, 68, 75, 96, 99, 107, 119, 136, 148, 158, 163, 204, 271, 272, 297, 311, 352
O. mozinnae Linell	2	75, 88
O. rufulum Gahan	1	181
Oemini		
Eudistenia costipennis Fall	1	138
Malacopterus tenellus (F.)	1	268
Oeme costata costata LeConte	1	249
O. rigida rigida (Say)	1	219
Paranoplium gracile gracile (LeConte)	3	60, 191, 285
P. g. laticolle (Linsley)	3	119, 168, 287
Opsimini		
Dicentrus bluthneri LeConte	1	225
Opsimus quadrilineatus Mannerheim	1	215
Piezocerini		
Piezocera serraticollis Linell	1	269
Plectromerini		

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Plectromerus dentipes (Olivier)	6	64, 76, 119, 211, 226, 324
Psebiiini		
Nathriobrium methioides Rice, Turnbow & Hovore	1	337
Nathrius brevipennis (Mulsant)	2	157, 172
Rhopalophorini		
Rhopalophora angustata Schaeffer	3	70, 74, 334
R. bicolorella Knull	2	170, 202
R. longipes (Say)	2	40, 64
R. meeskei Casey	2	238, 242
R. rugicollis (LeConte)	4	70, 74, 335, 336
Smodicini		
Smodicum cucujiforme (Say)	3	155, 208, 322
Stenopterini		
Callimoxys fuscipennis (LeConte)	1	122
C. sanguinicollis (Olivier)	1	117
C. s. sanguinicollis (Olivier)	3	119, 158, 305
Tillomorphini		
Euderces picipes (F.)	13	40, 63, 71, 107, 110, 145, 163, 166, 204, 226, 270, 311, 328
E. p. occidentalis Linsley	1	119
E. p. picipes (F.)	3	64, 162, 345

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
E. pini (Olivier)	26	38, 43, 64, 112, 117, 124, 145, 148, 155, 163, 165, 186, 204, 226, 268, 272, 273, 277, 297, 317, 318, 328, 343, 345, 347, 353
E. reichei LeConte	8	53, 68, 82, 268, 271, 273, 297, 352
Trachyderini		
Aethecerinus hornii (Lacordaire)	2	136, 161
A. latecinctus (Horn)	2	65, 91
A. wilsonii (Horn)	1	354
Ancylocera bicolor (Olivier)	4	119, 158, 161, 269
Batyle ignicollis (Say)	1	238
B. i. australis Linsley	1	136
B. i. ignicollis (Say)	2	196, 326
B. suturalis (Say)	2	158, 182
B. s. suturalis (Say)	3	268, 297, 353
Chemsakiella ricei (Chemsak)	1	67
Crioprosopus rimosus (Buquet)	2	87, 99
Crossidius ater LeConte	1	15
C. discoideus (Say)	1	24
Elytroleptus floridanus (LeConte)	3	136, 139, 148
Metaleptus batesi Horn	1	119
Purpuricenus axillaris Haldeman	1	126
P. dimidiatus LeConte	3	125, 137, 157
P. humeralis (F.)	1	345
P. paraxillaris MacRae	1	155

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Rhodoleptus femoratus (Schaeffer)	1	65
Schizax senex LeConte	1	176
Sphaenothecus bilineatus (Gray)	6	60, 75, 77, 88, 274, 319
Trachyderes mandibularis Audinet-Serville	2	272, 96
T. m. mandibularis Audinet-Serville	3	75, 267, 324
Tragidion armatum LeConte	1	7
T. auripenne Casey	3	58, 152, 272
T. gracilipes Linsley	1	288
T. peninsulare californicum Linsley	3	125, 127, 288
Lamiinae		
Acanthocinini		
Acanthocinus spectabilis (LeConte)	1	255
Astyleiopus variegatus (Haldeman)	11	64, 71, 73, 113, 116, 238, 270, 316, 349, 350, 360
Astylidius parvus (LeConte)	4	74, 274, 331, 343
Astylopsis collaris (Haldeman)	3	113, 256, 338
A. fascipennis Schiefer	1	345
A. macula (Say)	13	40, 43, 44, 110, 158, 162, 169, 209, 315, 325, 332, 345, 349
A. sexguttata (Say)	6	233, 238, 241, 253, 257, 332
Dectes sayi Dillon and Dillon	2	11, 14
D. texanus LeConte	1	72
Eutrichillus canescens Dillon	1	242
E. neomexicanus (Champlain and Knull)	1	248
Graphisurus despectus (LeConte)	2	158, 162

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
G. fasciatus (De Geer)	10	110, 119, 145, 155, 162, 181, 208, 257, 332, 355
Hyperplatys aspersa (Say)	3	40, 49, 358
H. californica Casey	1	348
H. maculata Haldeman	3	43, 110, 209
H. montana Casey	5	209, 292, 325, 340, 350
Leptostylopsis planidorsus (LeConte)	4	107, 140, 274, 361
L. terraecolor (Horn)	8	76, 85, 179, 197, 275, 324, 333, 361
Leptostylus gibbulosus Bates	1	352
L. hispidulus Bates	1	274
L. transversus (Gyllenhal)	6	64, 143, 150, 333, 350, 356
L. t. dietrichi Dillon	2	96, 337
L. t. floridellus Dillon	3	57, 324, 333
L. t. transversus (Gyllenhal)	4	158, 209, 332, 345
Lepturges angulatus (LeConte)	10	73, 82, 101, 158, 264, 268, 273, 292, 350, 356
L. a. angulatus (LeConte)	2	257, 270
L. a. canus Dillon	3	74, 75, 269
L. confluens (Haldeman)	6	10, 162, 163, 164, 165, 171
L. infilatus Bates	1	75
L. pictus (LeConte)	3	162, 270, 273
L. regularis (LeConte)	2	349, 350
L. symmetricus (Haldeman)	5	40, 171, 208, 209, 343
Neacanthocinus obliquus (LeConte)	4	244, 249, 251, 255
N. obsoletus (Olivier)	2	238, 257

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
N. pusillus Kirby	4	234, 241, 253, 256
Nyssodrysina haldemani (LeConte)	2	275, 333
Pseudastylopsis nebulosus (Horn)	1	231
Sternidius alpha (Say)	8	93, 107, 158, 162, 163, 181, 273, 292
S. crassulus LeConte	1	267
S. decorus (Fall)	1	119
S. mimeticus (Casey)	11	68, 71, 75, 76, 82, 85, 96, 97, 324, 325, 336
S. misellus (LeConte)	5	107, 148, 155, 297, 345
S. punctatus (Haldeman)	9	52, 110, 119, 160, 163, 171, 297, 345, 358
Sternidocinus barbarus (Van Dyke)	1	122
Styloleptus biustus (LeConte)	3	195, 268, 277
S. b. biustus (LeConte)	5	3, 38, 96, 209, 345
Urgleptes celtis (Schaeffer)	1	75
U. facetus (Say)	2	205, 296
U. foveatocollis (Hamilton)	2	85, 175
U. querci (Fitch)	22	64, 107, 112, 113, 126, 162, 165, 166, 169, 171, 192, 193, 205, 209, 292, 311, 318, 331, 343, 345, 349, 360
U. signatus (LeConte)	11	39, 105, 116, 117, 158, 181, 280, 311, 331, 343, 358
<u>Acanthoderini</u>		

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Aegomorphus modestus (Gyllenhal)	10	96, 110, 185, 193, 209, 257, 295, 304, 345, 356
Agapanthiini		
Hippopsis lemniscata (F.)	3	11, 12, 30
Spalacopsis filum (Klug)	1	210
Anisocerini		
Thryallis undatus (Chevrolat)	4	68, 75, 99, 268
Cyrtinini		
Cyrtinus beckeri Howden	1	341
C. pygmaeus (Haldeman)	7	63. 93, 107, 110, 145, 148, 155
Desmiphorini		
Desmiphora aegrota Bates	1	207
Eupogonius pauper LeConte	11	40, 43, 46, 63, 71, 123, 155, 209, 318, 331, 332, 337, 345
E. subarmatus (LeConte)	2	208, 209
E. tomentosus (Haldeman)	3	241, 254, 256
Psenocerus supernotatus (Say)	8	46, 193, 202, 297, 316, 332, 357, 360
Tigrinestola tigrina (Skinner)	2	83, 338
Dorcaschematini		
Dorcaschema alternatum (Say)	2	277, 278
D. cinereum (Olivier)	5	43, 63, 158, 162, 277
D. nigrum (Say)	2	160, 158
D. wildi Uhler	1	276
Hemilophini		

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Cathetopteron amoena Hamilton	1	269
Hemierana marginata (F.)	1	30
H. m. ardens (LeConte)	1	30
Mesosini		
Synaphaeta guexi (LeConte)	5	103, 172, 203, 287, 302
Moneilemini		
Moneilema armatum LeConte	1	35
Monochamini		
Goes debilis LeConte	3	119, 123, 142
G. pulcher (Haldeman)	2	119, 158
G. pulverulentus (Haldeman)	6	117, 146, 148, 151, 155, 257
G. tesselatus (Haldeman)	1	119
G. tigrinus (Degeer)	1	119
Hebestola nebulosa Haldeman	1	119
Microgoes oculatus (LeConte)	3	63, 105, 257
Monochamus carolinensis (Olivier)	3	238, 253, 257
M. clamator lator Casey	1	231
M. c. linsleyi Dillon and Dillon	1	249
M. marmorator Kirby	1	229
M. mutator LeConte	5	231, 241, 253, 255, 256
M. notatus (Drury)	4	236, 241, 253, 256
M. obtusus fulvomaculatus Linsley	2	244, 255
M. o. obtusus Casey	3	240, 252, 260
M. scutellatus (Say)	4	241, 253, 256, 257
M. s. scutellatus (Say)	5	229, 236, 253, 256, 260
M. titillator (F.)	1	257
Neoptychodes trilineatus (L.)	2	272, 274

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Plectrodera scalator (F.)	1	199
Onciderini		
Lochmaeocles cornuticeps cornuticeps (Schaeffer)	1	75
L. tessellatus (Thomson)	2	61, 267
Oncideres cingulata (Say)	16	40, 44, 52, 53, 71, 95, 158, 160, 163, 165, 198, 206, 208, 299, 313, 316
O. pustulata LeConte	4	68, 75, 78, 99
O. rhodosticta Bates	2	88, 89
Parmenini		
Parmenosoma griseum Schaeffer	2	8, 36
Phytoeciini		
Mecas pergrata (Say)	1	16
Oberea bimaculata (Olivier)	3	358, 300, 314
O. gracilis (F.)	2	123, 131
O. myops Haldeman	2	56
O. ocellata Haldeman	1	300
O. quadricallosa LeConte	2	198, 206
O. ruficollis (F.)	2	188, 189
Oberea sp. Mulsant	23	21, 23, 27, 28, 29, 41, 42, 43, 50, 51, 102, 177, 178, 266, 289, 295, 300, 303, 304, 309, 310, 322, 358
Pogonocherini		
Callipogonius cornutus Linsley	1	202
Ecyrus arcuatus Gahan	5	64, 82, 84, 96, 268
E. dasycerus (Say)	2	187, 360

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
E. d. dasycerus (Say)	6	145, 155, 204, 268, 273, 347
E. d. floridanus Linsley	4	76, 140, 275, 324
E. penicillatus Bates	1	68
Lypsimena fuscata Haldeman	1	136
Pogonocherus mixtus Haldeman	3	233, 253, 256
P. propinquus Fall	1	246
Poliaenus obscurus schaefferi Linsley	1	249
P. oregonus (LeConte)	1	231
Pteropliini		
Ataxia crypta (Say)	1	97
A. falli Breuning	1	85
A. hubbardi Fisher	6	13, 25, 26, 30, 31, 173
Saperdini		
Saperda calcarata Say	3	198, 201, 202
S. candida F.	1	105
S. discoidea F.	2	158, 162
S. fayi Bland	1	295
S. horni Joutel	1	202
S. imitans Felt and Joutel	1	338
S. inornata Say	2	198, 202
S. lateralis F.	7	64, 110, 162, 257, 316, 331, 338
S. mutica Say	1	202
S. populnea moesta LeConte	2	198, 202
S. puncticollis Say	1	360
S. tridentata Olivier	1	316
S. vestita Say	1	209

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
Tetraopini		
Tetraopes femoratus LeConte	1	174
T. melanurus Schönherr	1	174
T. quinquemaculatus Haldeman	1	174
T. tetrophthalmus (Forster)	1	174
Lepturinae		
Desmocerini		
Desmocerus aureipennis cribripennis Horn	1	48
D. palliatus (Forster)	1	47
Encyclopini		
Encyclops caerulea (Say)	1	257
Leptalia macilenta (Mannerheim)	2	306, 342
Pyrotrichus vitticollis LeConte	1	321
Lepturini		
Analeptura lineola (Say)	8	56, 105, 117, 119, 188, 256, 257, 299
Anastrangalia laetifica (LeConte)	1	255
Anoplodera pubera (Say)	2	257, 345
Bellamira scalaris (Say)	4	106, 119, 257, 338
Brachyleptura champlaini Casey	1	254
B. circumdata (Olivier)	1	105
B. dehiscens (LeConte)	1	260
B. rubrica (Say)	5	105, 109, 112, 193, 338
B. vagans (Olivier)	3	238, 254, 257
Dorcasina grossa (LeConte)	1	216
Grammoptera exigua (Newman)	1	198, 209
G. haematites (Newman)	3	108, 119, 338
G. militaris (Chevrolat)	1	342

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
G. rhodopus (LeConte)	1	287
Judolia sexspilota (LeConte)	1	220
Leptalia macilenta (Mannerheim)	1	122
Leptura abdominalis (Haldeman)	1	219
L. hovorei Linsley and Chemsak	1	247
L. kerniana Fall	2	238, 255
L. obliterata (Haldeman)	1	261
L. o. deleta (LeConte)	1	254
L. plebeja Randall	1	257
L. subhamata Randall	2	256, 263
Lepturopsis biforis (Newman)	1	113
Neobellamira delicata australis Linsley and Chemsak	3	103, 138, 184
Ortholeptura insignis (Fall)	2	104, 118
O. valida (LeConte)	3	216, 231, 247
Pygoleptura brevicornis (LeConte)	2	243, 251
Stenelytrana emarginata F.	4	45, 147, 155, 193
Stictoleptura canadensis (Olivier)	1	132
Strangalepta abbreviata (Germar)	4	113, 119, 254, 263
Strangalia acuminata (Olivier)	4	51, 102, 119, 301
S. bicolor (Swederus)	1	338
S. famelica Newman	2	106, 119
S. luteicornis (F.)	2	51, 107
Strophiona nitens (Forster)	2	113, 119
Trachysida mutabilis (Newman)	2	190, 344
Trigonarthris minnesotana (Casey)	2	119, 257
T. proxima (Say)	1	44
Typocerus acuticauda acuticauda Casey	2	119, 204
T. deceptus Knull	1	119

Table 2.3 (cont.).

Taxomony	# plant taxa	Host plant code
T. velutinus (Olivier)	1	106
T. v. velutinus (Olivier)	3	114, 193, 205
Xestoleptura crassipes (LeConte)	3	118, 202, 261
Rhagiini		
Acmaeops discoideus (Haldeman)	1	257
A. marginatus (F.)	1	121
A. proteus (Kirby)	3	241, 253, 256
Anthophylax attenuatus (Haldeman)	2	117, 347
A. viridis LeConte	3	105, 116, 338
Brachysomida californica (LeConte)	1	1
B. vittigera Linsley and Chemsak	1	2
Centrodera decolorata (Harris)	2	119, 181
C. osburni Knull	1	284
Evodinus monticola (Randall)	1	262
Gaurotes cyanipennis (Say)	3	169, 277, 311
Pachyta armata LeConte	1	250
Pidonia ruficollis (Say)	3	116, 181, 338
P. scripta (LeConte)	1	338
Rhagium inquisitor (L.)	3	255, 256, 257
Stenocorus alteni Giesbert & Hovore	1	137
S. vestitus (Haldeman)	1	261
Xylosteini		
Leptorhabdium pictum (Haldeman)	1	158
Necydalinae		
Necydalis barbarae Rivers	1	127
N. cavipennis LeConte	1	132
N. mellita (Say)	3	113, 119, 257
Ulochaetes leoninus LeConte	1	255

Table 2.3 (cont.).

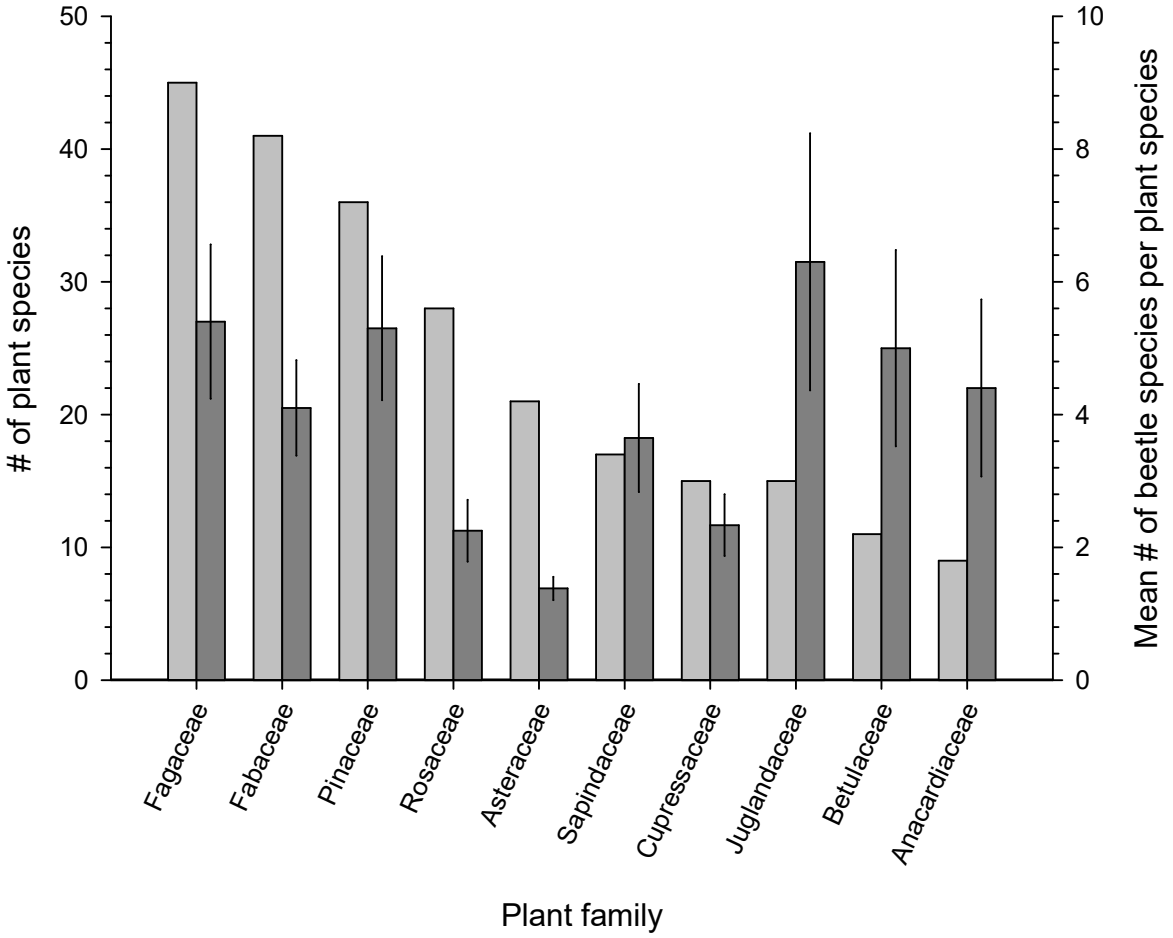
Taxomony	# plant taxa	Host plant code
Parandrinae		
Parandrini		
Neandra brunnea (F.)	3	116, 155, 202
N. marginicollis (Schaeffer)	1	167
Parandra polita Say	1	117
Prioninae		
Callipogonini		
Trichocnemis pauper (Linsley)	3	122, 138, 157
T. spiculatus neomexicanus Casey	1	238
T. s. spiculatus (LeConte)	1	240
Macrotomini		
Archodontes melanopus (L.)	1	119
Mallodon dasystomum (Say)	1	119
M. d. dasystomum (Say)	3	274, 264, 333
Neomallodon arizonicus (Casey)	1	119
Meroscelisini		
Tragosoma depsarium (L.)	3	249, 254, 256
Prionini		
Derobrachus brevicollis Audinet-Serville	1	119
Orthosoma brunneum (Forster)	2	112, 256
Prionus imbricornis (L.)	1	119
P. integer LeConte	2	15, 20
P. lecontei Lameere	1	129
P. pocularis Dalman in Schoenherr	1	238
Solenopterini		
Elateropsis rugosus Gahan	2	324, 333
Sphenostethus taslei (Buquet)	4	113, 114, 117, 119
Spondylidinae		

Table 2.3 (cont.).

Taxomony	**# plant taxa**	**Host plant code**
Asemini		
Arhopalus rusticus hesperus Chemsak and Linsley	1	249
A. r. obsoletus (Randall)	1	238
Asemum striatum (L.)	5	233, 241, 254, 256, 257
Megasemum asperum (LeConte)	1	261
Tetropium abietis Fall	1	231
T. cinnamopterum Kirby	3	241, 253, 256
Atimiini		
Atimia confusa confusa (Say)	1	224
A. c. dorsalis LeConte	2	214, 216
A. c. maritima Linsley	1	215
A. vandykei Linsley	1	222
Saphanini		
Michthisoma heterodoxum LeConte	1	208
Disteniidae		
Disteniinae		
Elytrimitatrix undata (F.)	3	63, 257, 316

Figures

Fig. 2.1. Number of plant species per plant family that were recorded as host of cerambycid beetles (light grey bars, Y axis on the left) for the ten plant families associated with the greatest number of beetle species (from Table 2.2), and the mean (± 1 SE) number of beetle species recorded per plant species within families (dark grey bars, Y axis on the right).



CHAPTER 3: AN EVALUATION OF METHODS USED FOR FIELD BIOASSAYS FOR TESTING ATTRACTION OF CERAMBYCID BEETLES TO SYNTHESIZED PHEROMONES

Abstract

Here we describe several field experiments which evaluated potential problems with current methods of trapping cerambycid beetles using panel traps baited with synthesized pheromones. The first experiment demonstrated that beetles were not attracted to unbaited traps, and unlikely to be captured passively by traps, and also confirmed that the solvent commonly used in diluting synthesized pheromone (isopropanol) has no activity as an attractant. The second experiment showed that positioning traps at least 5 m apart in transects was effective in preventing interference between treatments, such as when unbaited traps intercept flying beetles that are attracted to a neighboring trap. The third experiment confirmed that not all components of the pheromone are individually attractive, and the addition of stereoisomers not present in the natural blend can hinder attraction. Finally, the fourth experiment showed that increasing the release rate of pheromone emitters usually will result in greater numbers of beetles being attracted to traps. The findings of these experiments generally validate current methods of trapping cerambycids, but also suggest that trap efficiency may be further improved by optimizing release rates of pheromone emitters.

Introduction

A variety of trap designs have been devised for capturing wood-boring beetles over the last several decades, including black light, glue, stovepipe, sticky, flight-intercept, panel, and multiple funnel traps (e.g., Stewart and Lam 1970, Lindgren 1983, Chénier and Philogène 1989,

Czokajlo et al. 2003, Lacey et al. 2004, Bouget et al. 2008, Miller and Crowe 2011, Allison et al. 2014). In recent years, a considerable amount of research has been devoted to improving the efficiency with which traps of these general designs catch beetles, such as by altering their dimensions, color, height above the ground, and applying surface lubricants that render traps more slippery (e.g., Wermelinger et al. 2007; Miller and Crowe 2009, 2011; Allison et al. 2011; Graham et al. 2010). The earliest trap baits developed for cerambycids were plant volatiles, with ethanol and monoterpenes proving to be effective attractants for many species whose larvae develop in conifers (reviewed by Millar and Hanks 2016). Synthetic pheromones of cerambycids can be very effective attractants for targeting species which otherwise are rarely if ever encountered (e.g., Ray et al. 2009, 2014), and blends of pheromones of different species have been devised as multi-species lures that attract a diversity of species simultaneously to traps (e.g., Hanks et al. 2012, Hanks and Millar 2013).

Optimized methods of dispensing attractant chemicals are critical for improving trap catch. Few beetles may be attracted to traps if release rates are too low (e.g., Lacey et al. 2007), while very high release rates have unknown effects. A common release device for synthesized plant volatiles has been polyethylene bags (e.g., Miller et al. 2011), while synthetized pheromones of adult cerambycids have been dispensed from rubber septa, cotton wicks (alone, within glass vials, or stopping vials), glass vials (open or partially sealed), and polyethylene sachets (e.g., Lacey et al. 2009, Graham et al. 2010, Hanks et al. 2014). However, there has been very little research to optimize the efficiency of pheromone lures for cerambycids, particularly by assessing the influence of release rate on the numbers of beetles that are attracted to traps.

In this article, we describe four field experiments which evaluated potential problems with current methods of trapping cerambycid beetles using pheromone-baited panel traps.

Experiment 1 assessed attraction of beetles to unbaited traps, passive capture by traps, and whether the solvent commonly used in diluting synthesized pheromone (isopropanol) was itself an attractant. Experiment 2 assessed the potential for interference among trap treatments within transects, to determine the distance between traps that is necessary to prevent interference, such as when beetles that are attracted to one trap are intercepted by another nearby trap. Experiment 3 tested the hypothesis that certain pheromone components are apparently ineffective as attractants is due to being out-competed by stronger attractants during field bioassays. Finally, Experiment 4 tested the effect of pheromone release rate on number of beetles caught by traps, to determine whether trap catch could be optimized by altering release rate.

Materials and Methods

Sources of chemicals.

Racemic *syn*- and *anti*-2,3-hexanediols were synthesized as described by Lacey et al. (2004, 2007). Other compounds were purchased from commercial sources, including 3-hydroxyhexan-2-one, (5*E*)-6,10-dimethyl-5,9-undecadien-2-ol (termed fuscumol), (5*E*)-6,10-dimethyl-5,9-undecadien-2-yl acetate (fuscumol acetate), 2-(undecyloxy)ethanol (monochamol; Bedoukian Research, Inc., Danbury, CT), citral, *S*-limonene, 2-phenylethanol, and racemic 2-methylbutan-2-ol (Aldrich Chemical, Milwaukee, WI), nerol (Fluka Analytics, Steinheim, Germany), and (*S*)-2-methylbutan-1-ol (TCI America, Boston, MA).

General methods of trapping.

Field experiments were conducted at seven sites in east-central Illinois, with a mix of "virgin", second growth, and old growth forests, and one urban location, with the forests being

mostly dominated by oaks, hickories, and maples (Table 3.1). Beetles were trapped with panel traps (black corrugated plastic, 1.2 m high × 0.3 m wide, Alpha Scents Inc., West Linn, OR) which were coated with the fluoropolymer dispersion Fluon® (Northern Products, Woonsocket, RI), and hung from inverted L-shaped frames constructed of polyvinyl chloride pipe (for details, see Graham et al. 2010). Trap basins contained ~300 ml of saturated aqueous NaCl solution to kill and preserve trapped beetles. Traps were serviced every 1 to 3 d, at which time treatments usually were rotated within transects to control for positional effects (see below).

Trap lures usually consisted of polyethylene sachets (press-seal bags, Bagette™ model 14770, 5.1 cm x 7.6 cm, 0.05 mm wall thickness, Cousin Corp., Largo, FL) which were loaded with 0.25 mg/enantiomer of pheromone diluted in 1 ml of solvent (ethanol in 2010, subsequently isopropanol). Control traps usually were baited with lures containing only solvent (see below).

Taxonomy of trapped beetles follows Monné and Hovore (2005). Representative specimens of all the species captured are available from the laboratory of LMH, and voucher specimens have been deposited with the collection of the Illinois Natural History Survey, Champaign, IL.

Targeted species.

The field experiments targeted four species in the subfamily Cerambycinae (all tribe Clytini) and two species in the subfamily Lamiinae (Acanthocinini), all of which are among the most common and abundant cerambycids in the midwestern United States (Hanks et al. 2014), including:

1) *Neoclytus acuminatus acuminatus* (F.) (Cerambycinae), pheromone composed solely of (2*S*,3*S*)-2,3-hexanediol (Lacey et al. 2004);

2) *Neoclytus mucronatus mucronatus* (F.) (Cerambycinae), pheromone composed solely of (*R*)-3-hydroxyhexan-2-one (Lacey et al. 2007);

3) *Megacyllene caryae* Gahan (Cerambycinae), pheromone composed of (*S*)-(–)-limonene, 2-phenylethanol, (–)-α-terpineol, nerol, neral, geranial, (2*S*,3*R*)- and (2*R*,3*S*)-2,3-hexanediol, and (*S*)-2-methylbutan-2-ol (Lacey et al. 2008, unpub. data);

4) *Xylotrechus colonus* (F.) (Cerambycinae), pheromone composed of (*R*)- and (*S*)-3-hydroxyhexan-2-one, (2*S*,3*S*)- and (2*R*,3*R*)-2,3-hexanediol, and (2*R*,3*S*)- and (2*S*,3*R*)-2,3-hexanediol (Lacey et al. 2009, unpub. data).

5) *Astylidius parvus* (LeConte) (Lamiinae), pheromone composed of (*R*)- and (*S*)-fuscumol, and (*R*)-fuscumol acetate (Meier et al. 2016);

6) *Lepturges angulatus* (LeConte), (Lamiinae), pheromone composed of (*R*)- and (*S*)-fuscumol acetate (Meier et al. 2016).

Field Experiments.

Experiment 1 assessed the degree to which adult cerambycids are drawn visually to unbaited panel traps, or flying beetles are intercepted passively by unbaited traps, and whether the solvent isopropanol is itself an attractant. The experimental design consisted of two traps, positioned ~10 m apart, one of which had a lure that contained 1 ml isopropanol, the other with an empty lure. Two pairs of traps (at least 50 m apart) were set up at each of the Brownfield Woods, Forest Glen Preserve, Robert Allerton Park, and Trelease Woods sites (Table 3.1) during 12 June to 29 July 2013, for a total of 8 pairs of traps. To confirm that beetles of a particular species were active during the study, trap catch was compared with that of pheromone-baited traps in other field bioassays that were running at the same time and at the same sites. The

sources of these data are as follows: experiment targeting *N. a. acuminatus* (Robert Allerton Park, lure treatment (2*R*,3*R*)-2,3-hexanediol + racemic fuscumol + fuscumol acetate); experiment targeting *X. colonus* (Robert Allerton Park, lure treatment 3-hydroxyhexan-2-one + racemic 2-methylbutan-1-ol); experiment targeting *A. parvus* and *L. angulatus* (Trelease Woods, 3-hydroxyhexan-2-one + racemic fuscumol + fuscumol acetate + monochamol).

Experiment 2 assessed the potential for traps to interfere with one another, such as when an unbaited trap intercepts beetles that are flying to a neighboring trap which is baited with an attractant. The potential for interference was tested by surrounding a pheromone-baited trap with unbaited traps at increasing distances. The study first targeted *M. caryae*, with the central trap baited with citral (an isomeric blend of the pheromone components neral and geranial, and a strong attractant of this species; e.g., Handley et al. 2015) + *anti*-2,3-hexanediol diluted in ethanol. Unbaited traps were positioned so as to radiate out from the central baited trap, with a line of traps in each of the four cardinal directions, each line having traps at distances of 1, 5, 10, and 20 m from the center (N = 16 unbaited traps). The experiment was conducted at Forest Glen Preserve and Robert Allerton Park during 10 to 29 April 2010 with one transect at each location, replicated over time. A second trial targeted *N. a. acuminatus*, with the central trap baited with racemic *syn*-2,3-hexanediol, and again four lines of unbaited traps that were 1, 5, and 10 m from the center (N = 12 traps). That experiment was conducted at the same two study sites during 26 May to 4 June 2010, again with one transect at each location and replicated over time.

Experiment 3 tested the hypothesis that the apparent inactivity of some pheromone components during field bioassays is an artifact of experimental design: that is, traps baited with these weak attractants are out-competed by neighboring traps within the same transect that are baited with stronger attractants. The experiment first targeted *M. caryae*, the strong attractant

being citral and the supposedly non-attractive test compounds being the pheromone components (*S*)-(–)-limonene and (*S*)-2-methylbutan-2-ol (in racemic 2-methylbutan-2-ol). The two compounds were tested in separate experiments. The experimental design involved two pairs of traps which were separated by at least 100 m and baited as follows (traps within a pair separated by 10 m): 1) one trap baited with the test compound and the other with a solvent control lure; 2) one trap baited with the test compound and other baited with citral. The hypothesis therefore would be confirmed if the test compound attracted significant numbers of beetles (relative to the control) only in the absence of traps baited with citral. The experiment was conducted at Forest Glen Preserve during 24 April to 20 May 2013. One transect of each pheromone component was set up, traps were serviced every 1-3 d, at which time treatments were rotated within and between pairs of traps to account for positional bias.

A second trial of Experiment 3 targeted *X. colonus*, testing the effect of the highly attractive racemic 3-hydroxyhexan-2-one on attraction of beetles to two apparently inactive components (tested separately): *syn*- and *anti*-2,3-hexanediol (see Lacey et al. 2009, Hanks et al. 2012). The experimental design was as already described, but with a control trap added to the pair of traps that included the 3-hydroxyhexan-2-one treatment (to allow a more direct test for significant attraction to the test compounds). This experiment was conducted at Forest Glen Preserve and Nettie Hart Woods during 23 June to 30 August 2014, with one transect at each location replicated over time.

A third trial of Experiment 3 targeted *N. a. acuminatus*, but had a somewhat different objective. Lacey et al. (2004) found that attraction of the adults of this species to the synthesized pheromone, (2*S*,3*S*)-2,3-hexanediol, was not influenced by the presence of the *R,R*-enantiomer, but apparently was strongly antagonized by one or both of the diastereomers. Nevertheless, the

apparent inactivity of the blend of all four stereoisomers during bioassays may have been due to competition from neighboring traps that were baited with the strongly attractive *SS*-enantiomer. That hypothesis was tested using the same method as used for *X. colonus*, with the blend of all four stereoisomers being the test compound and racemic *syn*-hexanediol being the strong attractant. The experiment was conducted at Robert Allerton Park during 28 June to 12 July 2012, with one transect replicated over time.

Three independent trials of Experiment 4 tested the relationship between release rate of synthesized pheromones from lures and the number of beetles caught. The first trial targeted both *N. m. mucronatus* and *X. colonus* using traps baited with racemic 3-hydroxyhexan-2-one. Lure release rate was manipulated by adjusting the dilution of pheromone in 1 ml of ethanol by powers of two, with treatments being 0, 12.5, 25, 50, and 100 mg of pheromone. A preliminary laboratory experiment confirmed that release rate was positively and linearly correlated with the concentration of pheromone within lures (unpub. data). A sixth treatment was a pair of 50 mg lures, in case release rate would be increased further by doubling the surface area of lures. The experiment was conducted at Forest Glen Preserve and Trelease Woods during 9 August to 13 September 2010, with two transects at Forest Glen and one transect at Trelease Woods replicated over time.

The second trial of Experiment 4 did not target any particular species, the traps being baited with a blend of synthetized pheromones which had been developed to attract a diversity of cerambycid species (Hanks et al. 2012, Hanks and Millar 2013). The six-component blend was composed of synthesized compounds that are typical pheromone components of species in the subfamily Cerambycinae (racemic 3-hydroxyhexan-2-one, *syn*-2,3-hexanediol, racemic 2-methylbutan-1-ol), and of species in the subfamily Lamiinae (racemic fuscumol, racemic

fuscumol acetate, monochamol; see Millar and Hanks 2016). Release rate was manipulated by increasing the dose of the blend by powers of five dissolved in 1 ml isopropanol, with treatments being 0, 2.2, 11, 55 and 275 mg. The experiment was conducted during 8 August to 28 September 2012 with one transect set out at Vermilion River Observatory. Only adults of *X. colonus* were caught in numbers sufficient for statistical analysis.

A third trial of Experiment 4 specifically targeted lamiine species by baiting traps with racemic fuscumol and fuscumol acetate. Several species of lamiines in the eastern U. S. are known to be attracted by one or both of these compounds (Mitchell et al. 2011, Hanks and Millar 2013, Meier et al. 2016). This experiment used lures of a different design than those of the other experiments, being constructed from polyethylene tubing (5 cm wide, Associated Bag Company, Milwaukee, WI) that was cut to a length of 7 cm and heat sealed on each end. A preliminary study revealed that the release rates of lures loaded with 1 ml of neat compound (fuscumol and fuscumol acetate in separate lure) could be manipulated by varying the wall thickness of the tubing and by adding a cotton wick (#2 medium dental, Patterson Dental Supply, Montreal, Quebec), as follows: 1) 38 µm thickness with no wick, 2) 152 µm thickness with no wick, 3) 38 µm thickness + wick, 4) 152 µm thickness + wick. Experiments in the laboratory revealed that lure bags released fuscumol at rates of ~30, 15, 8, and 3 mg/d respectively, and fuscumol acetate at rates of ~80, 50, 20, and 10 mg/d (unpub. data). Controls were 152 µm lures containing a clean cotton roll. For comparative purpose, we also included a sixth treatment: the commercially available polyethylene sachets that were used in the other experiments (56 µm wall thickness), also loaded with 1 ml of neat compounds (release rates ~27 and 60 mg/d for fuscumol and fuscumol acetate). Thus, release rates of the sachets approximated the highest release rates of the lures created from polyethylene tubing. The field bioassay comprised of a linear transect of six

traps, one baited with each lure type. The experiment was conducted at Robert Allerton Park and Forest Glen Preserve, with one transect at each location, during 28 Jun to 22 July 2013. During this trial, only the lamiines *A. parvus* and *L. angulatus* were captured in numbers sufficient for statistical analysis.

Statistical analysis.

Differences between treatment means, blocked by site and collection date, were tested using the non-parametric Friedman's Test (PROC FREQ, option CMH; SAS Institute 2008) because data violated assumptions of ANOVA (Sokal and Rohlf 1995), having non-normal distribution and unequal variances. Pairs of treatment means for lures were compared using the non-parametric Ryan-Einot-Gabriel-Welsch Q (REGWQ) multiple comparison test (SAS Institute 2011). Tukey's multiple comparisons test was used in Experiment 2 due to unequal sample sizes within replicates.

Results

During Experiment 1, unbaited traps, and those baited with lures which contained only the solvent isopropanol, captured a total of 55 cerambycid beetles of 20 species during the 45 d period, with very small numbers of each species (mean [± 1 SD] total number of beetles per species: 0.3 ± 0.09 and 0.4 ± 0.07 beetles per replicate, respectively). This low trap catch was not due to the scarcity of beetles. For example, pheromone baited traps in a different but concurrent study, conducted at Robert Allerton Park and Trelease Woods, caught 62, 66, 25, and 66 adults of *N. a. acuminatus*, *X. colonus*, *A. parvus*, and *L. angulatus*, respectively, during which time the solvent baited traps of the present study caught no beetles of these species, while unbaited traps

caught only two adults of *X. colonus* (<1% of the beetles caught in the other experiment). Overall, traps baited with pheromones in the same period at the two locations caught a mean number of beetles (± 1 SD) of 2.9 ± 0.1. A comparison of the means of the isopropanol-baited and unbaited traps against the traps baited with pheromones shows that the means were not equal (pheromones vs. unbaited: $Q_{1,905} = 30.9$, $P < 0.0001$; pheromones vs. isopropanol: $Q_{1,905} = 27.0$, $P < 0.0001$), and the means of the isopropanol-baited and unbaited traps were not different ($Q_{1,150} = 2.14$, $P = 0.15$).

In Experiment 2, most of the beetles that were trapped apparently were quite accurate in locating the source of attractants, the pheromone lures in the central traps. Of 206 adults of *M. caryae*, 168 (82%) were captured in the central trap, 36 (17%) were captured in unbaited traps that were 1 m from the center, and only 2 beetles (1%) were caught by unbaited traps at greater distances (Fig. 3.1A). Similarly, 39 of 44 adults of *N. a. acuminatus* (88%) were captured by the central pheromone-baited trap, with traps that were 1 and 5 m away catching only two (5%) and three (7%) beetles, respectively, and no beetles in traps at greater distances (Fig. 3.1B).

During the first trial of Experiment 3, traps caught 495 adults of *M. caryae*. Traps baited with (*S*)-(–)-limonene caught few beetles regardless of whether they were paired with a trap baited with citral or a control trap (1 and 0 beetles, respectively; means not significantly different, excluding the mean for citral, Friedman's $Q_{2,21} = 2.33$, $P > 0.05$). The same was true for traps baited with 2-(*S*)-methylbutan-1-ol, with 0 beetles caught by traps paired with a trap baited with citral and 0 beetles when paired with a control trap ($Q_{2,9} = 0$, $P > 0.05$).

During the trial of Experiment 3 that targeted *X. colonus*, 59 adults of that species were caught by traps. For both the *syn*- and *anti*-2,3-hexanediol test compounds, similar numbers of beetles were captured by traps that were paired with the strong attractant 3-hydroxyhexan-2-one

and by traps paired with a control trap (Fig. 3.2), and the means of the *syn*- and *anti*-2,3-hexane diols were not different from the negative control in either case.

During the trial of Experiment 3 that targeted *N. a. acuminatus*, 117 beetles were caught. Traps baited with the generic blend of all four stereoisomers of 2,3-hexanediol attracted similar numbers of beetles regardless of whether they were paired with a trap baited with only the *syn*-enantiomers or with a control trap (Fig. 3.3). The mean numbers of beetles captured in traps baited with generic diols were not statistically different from one another, although the generic diol traps in the set without the strong attractant did not capture more beetles than the control traps.

During the first trial of Experiment 4, traps caught 289 adults of *N. m. mucronatus*, with the number per trap increasing in a nearly linear fashion with the concentration of 3-hydroxyhexan-2-one within lures (Fig. 3.4A). The treatment using two lures did not result in increased attraction. During the same experiment, 109 adults of *X. colonus* also were caught, but that species apparently was not strongly influenced by pheromone release rate, with similar numbers trapped regardless of pheromone dose (Fig. 3.4B).

During the trial of Experiment 4 that used the synthesized blend of various cerambycid pheromones, traps caught 26 adults of *X. colonus*. In contrast to the first trial, trap catch increased steadily with pheromone dose within lures to the maximum dose (Fig. 3.5).

During the trial of Experiment 4 that tested emission rates of fuscumol and fuscumol acetate, traps captured 25 and 31 adults of *A. parvus* and *L. angulatus*, respectively. The commercially available press-seal sachets caught the greatest number of *A. parvus*, but similar numbers were captured by traps baited with lures created from polyethylene tubing with wall thickness of 38 μm, with or without wick (Fig. 3.6A). The commercially available sachets also

caught the greatest number of *L. angulatus* (Fig. 3.6B).

Discussion

In general, methods used in past experiments have been sound, and the experiments presented validate currently used methods. Unbaited panel traps with control lures capture very few beetles, and therefore are effective for bioassays comparing attractiveness of semiochemicals. Traps within a line transect were also shown to have a very low chance of chemical interference between traps at a distance of 10 m, and the lure release rates of the sachets chosen for pheromone dissemination has been adequate for purposes of survey and experimentation. It was important to make sure all of the experiments set up previously were not erroneous so as to have confidence in all our results moving forward.

The findings from Experiment 1 confirm that unbaited panel traps, and traps baited only with the solvent isopropanol, capture cerambycid beetles in very small numbers. These findings suggest that the beetles are not drawn to traps by visual cues, such as would be the case if the dark silhouette of traps mimicked the visual profile of trees. Moreover, the study showed that beetles are unlikely to be caught passively by traps, with a low passive trap catch rate of 0.3 beetles per replicate, which argues against the notion that traps operate by intercepting beetles as they disperse through the forest. Comparing the diversity of cerambycids caught by traps baited with pheromones, isopropanol, and unbaited, resulted in Shannon Diversity Index (H') of 2.4, 0.1, and 0.06, respectively, suggesting that isopropanol-baited and unbaited traps are ineffective at attracting beetles.

Experiment 2 demonstrated that separating traps within transects by at least 10 m is sufficient to prevent interference between experimental treatments. Taken together, Experiments

1 and 2 validate the methods that currently are used for trapping cerambycids, in which panel traps are baited with pheromones diluted in isopropanol, and traps in transects are separated by at least 10 m (e.g., Handley et al. 2015, Hayes et al. 2015, Mitchell et al. 2015, Meier et al. 2016).

The findings of the trial of Experiment 3 which targeted *M. caryae* revealed that neither of the test compounds were active attractants, rejecting the hypothesis that the test compounds have activity as attractants which were overshadowed by stronger attractants during earlier field experiments. Similarly, the trial which targeted *X. colonus* demonstrated that both the *syn*- and *anti*-2-3-hexanediol components of the pheromone indeed have very little if any activity in attracting beetles when tested alone. The results of these two trials showed that not all pheromone components present in the pheromone blend of a cerambycid species act as attractants individually and, although their roles remain unknown, some may be important in the segregation of species (Mitchell et al. 2015). Finally, the trial that targeted *N. a. acuminatus* confirmed that the apparently weak attraction to the generic blend of the enantiomers of 2,3-hexanediol is not merely a consequence of its being outcompeted during field bioassays by traps baited with the strongly attractive *syn*- enantiomers. The experiment confirmed that the generic blend attracts significant numbers of *N. a. acuminatus*, but is a weak attractant, this result also suggests that the *anti*-2,3-hexanediols are acting as inhibitors of sorts, reducing the attraction of the *syn*-2,3-hexanediols.

Experiment 4 revealed that the numbers of cerambycid beetles which were attracted to traps generally increased with the rates at which synthesized pheromones were released by lures. Thus, in each case the possibility remains that trap catch could be improved still further by designing lures with even higher release rates. The efficacy of the commercially available sachets in attracting beetles of the two lamiine species suggests that it was fortuitous that the

sachets were chosen to be the standard lure type in earlier experiments (e.g. Graham et al.2010).

In summary, current methods of trapping cerambycid beetles with pheromone baited panel traps appear to be effective, providing a reliable assessment of relative attraction with minimal problems due to interference between treatments and inappropriate controls. The reliability of these methods is further attested to by the earlier experiments which had indicated that certain pheromone components of *M. caryae* and *X. colonus* are not attractants when tested alone (Lacey et al. 2008, Hanks and Millar 2013), as was confirmed here. Nevertheless, the findings from Experiment 4 suggest that trapping methods may be further improved by research on the design of pheromone lures, to optimize release rates.

Acknowledgments

We thank Steve Buck and the University of Illinois Committee on Natural Areas, the Champaign County Forest Preserves District, Vermilion County Conservation District, and the Illinois Department of Natural Resources for access to field sites. We appreciate funding support from The Alphawood Foundation of Chicago (to Lawrence M. Hanks), and the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service (grant No. 2009-35302-05047) and USDA-APHIS (grant No. 10-8100-1422-CA), both to Jocelyn G. Millar and LMH.

References

Allison, J. D., C. W. Johnson, J. R. Meeker, B. L. Strom, and S. M. Butler. 2011. Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. J. Econ. Entomol. 104: 1258-1264.

Allison, J. D., B. D. Bhandari, J. L. McKenney, and J. G. Millar. 2014. Design factors that influence the performance of flight intercept traps for the capture of longhorned beetles (Coleoptera: Cerambycidae) from the subfamilies Lamiinae and Cerambycinae. PLoS ONE 9: e93203.

Bouget, C., H. Brustel, A. Brin, and T. Noblecourt. 2008. Sampling saproxylic beetles with window flight traps: methodological insights. Rev. Écol. (Terre Vie), suppt. 10: 21–32.

Chénier, J.V.R., and B.J.R. Philogène 1989. Evaluation of three trap designs for the capture of conifer-feeding beetles and other forest Coleoptera. Can. Entomol. 121: 159–167.

Czokajlo, D., J. McLaughlin, L. I. Abu Ayyash, S. Teale, J. Wickham, J. Warren, R. Hoffman, B. Aukema, K. Raffa, and P. Kirsch. 2003. Intercept™ panel trap (INT PT) effective in management of forest Coleoptera, pp. 125-126. *In* M. L. McManus and A. M. Liebhold (eds.), Proceedings: Ecology, survey and management of forest insects. USDA For. Serv., Northeastern Res. Stn., Gen. Tech. Rep. 311, Newton Square, PA.

Graham, E. E., R. F. Mitchell, P. F. Reagel, J. D. Barbour, J. G. Millar, and L. M. Hanks. 2010. Treating panel traps with a fluoropolymer dramatically enhances their efficiency in capturing cerambycid beetles. J. Econ. Entomol. 103: 641–647.

Handley, K., J. Hough-Goldstein, L. M. Hanks, J. G. Millar, and V. D'Amico. 2015. Species richness and phenology of cerambycid beetles in urban forest fragments of northern Delaware. Ann. Entomol. Soc. Am. 108: 251–262.

Hanks, L. M., and J. G. Millar. 2013. Field bioassays of cerambycid pheromones reveal widespread parsimony of pheromone structures, synergism by host plant volatiles, and antagonism by components from heterospecifics. Chemoecology 23: 21–44.

Hanks, L. M., J. G. Millar, J. A. Mongold-Diers, J.C.H. Wong, L. R. Meier, P. F. Reagel, and R. F. Mitchell. 2012. Using blends of cerambycid beetle pheromones and host plant volatiles to simultaneously attract a diversity of cerambycid species. Can. J. For. Res. 42: 1050–1059.

Hanks, L. M., P. F. Reagel, R. F. Mitchell, J.C.H. Wong, L. R. Meier, C. A. Silliman, E. E. Graham, B. L. Striman, K. P. Robinson, J. A. Mongold-Diers, and J. G. Millar. 2014. Seasonal phenology of the cerambycid beetles of east-central Illinois. Ann. Entomol. Soc. Am. 107: 211–226.

Hayes, R. A., M. W. Griffiths, H. F. Nahrung, P. A. Arnold, L. M. Hanks, and J. G. Millar. 2016. Optimizing generic cerambycid pheromone lures for Australian biosecurity and biodiversity monitoring. J. Econ. Entomol. (in press).

Lacey, E. S., M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2004. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus acuminatus acuminatus*. J. Chem. Ecol. 30: 1493–1507.

Lacey, E. S., J. A. Moreira, J. G. Millar, A. M. Ray, and L. M. Hanks. 2007. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus mucronatus mucronatus*. Entomol. Exp. Appl. 122: 171–179.

Lacey, E. S., J. A. Moreira, J. G. Millar, and L. M. Hanks. 2008. A male-produced aggregation pheromone blend consisting of alkanediols, terpenoids, and an aromatic alcohol from the cerambycid beetle *Megacyllene caryae*. J. Chem. Ecol. 34: 408–417.

Lacey, E. S., J. G. Millar, J. A. Moreira, and L. M. Hanks. 2009. Male-produced aggregation pheromones of the cerambycid beetles *Xylotrechus colonus* and *Sarosesthes fulminans*. J. Chem. Ecol. 35: 733–740.

Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. 115: 299–302.

Meier, L. R., Y. Zou, J. G. Millar, J. A. Mongold-Diers, and L. M. Hanks. 2016. Synergism between enantiomers creates species-specific pheromone blends and minimizes cross-attraction for two species of cerambycid beetles. J. Chem. Ecol. (in press).

Millar, J. G., and L. M. Hanks. 2016. Chemical ecology of cerambycid beetles. *In* Q. Wang (ed.) Cerambycidae of the world: biology and pest management. CRC Press/Taylor & Francis, Boca Raton, FL (in press).

Miller, D. R., and C. M. Crowe. 2009. Length of multiple-funnel traps affects catches of some bark and wood boring beetles in a slash pine stand in northern Florida. Fla. Entomol. 92: 506–507.

Miller, D. R., and C. M. Crowe. 2011. Relative performance of Lindgren multiple-funnel, intercept panel, and Colossus pipe traps in catching Cerambycidae and associated species in the southeastern United States. J. Econ. Entomol. 104: 1934–1941.

Mitchell, R. F., E. E. Graham, J.C.H. Wong, P. F. Reagel, B. L. Striman, G. P. Hughes, M. A. Paschen, M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2011. Fuscumol and fuscumol acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. Entomol. Exp. Appl. 141: 71–77.

Mitchell, R. F., P. F. Reagel, J.C.H. Wong, L. R. Meier, W. Dias Silva, J. Mongold-Diers, J. G. Millar, and L. M. Hanks. 2015. Cerambycid beetle species with similar pheromones are

segregated by phenology and minor pheromone components. J. Chem. Ecol. 41: 431-440.

Monné, M. A., and F. T. Hovore. 2005. Checklist of the Cerambycidae (Coleoptera) of the Western Hemisphere. BioQuip, Rancho Dominguez, CA.

Ray, A. M., J. G. Millar, J. S. McElfresh, I. P. Swift, J. D. Barbour, and L. M. Hanks. 2009. Male-produced aggregation pheromone of the cerambycid beetle *Rosalia funebris*. J. Chem. Ecol. 35: 96–103.

Ray, A. M., R. A. Arnold, I. Swift, P. A. Schapker, S. McCann, C. J. Marshall, J. S. McElfresh, and J. G. Millar. 2014. (*R*)-desmolactone is a sex pheromone or attractant for the endangered valley elderberry longhorn beetle *Desmocerus californicus dimorphu*s and several congeners (Cerambycidae: Lepturinae). PLoS One 9: e115498.

SAS Institute. 2011. SAS/STAT Users Guide release 9.3. SAS Institute, Cary, NC.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

Stewart, P. A., and J. J. Lam, Jr. 1970. Capture of forest insects in traps equipped with blacklight lamps. J. Econ. Entomol. 63: 871–873.

Wermelinger, B., P. F. Fluckiger, M. K. Obrist, and P. Duelli. 2007. Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. J. Appl. Entomol. 131: 104–114.

Tables

Table 3.1. Study sites for field experiments conducted in east-central Illinois during 2010-2014.

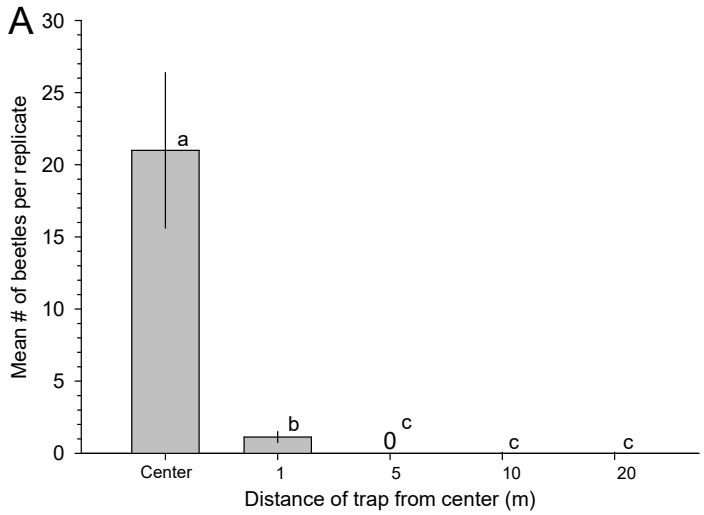
County	Site	GPS coordinates (lat., long.)	Area (ha)
Champaign	Brownfield Woods[1]	40.145, -88.165	26
	Nettie Hart Memorial Woods[1]	40.229, -88.358	16
	Private residence in Urbana, IL	40.0970, -88.2032	0.1
	Trelease Woods[1]	40.132, -88.141	29
Piatt	Robert Allerton Park[1]	39.996, -88.651	600
Vermilion	Forest Glen Preserve[2]	40.081, -87.545	3
	Vermilion River Observatory[1]	40.066, -87.561	192

[1]University of Illinois (http://research.illinois.edu/cna/)

[2]Vermilion County Conservation District (http://www.vccd.org/)

Figures

Fig. 3.1. Mean (± 1 SE) number of adult beetles caught during Experiment 2 by a pheromone baited trap (center) and unbaited traps that were positioned at increasing distances from the center in the four cardinal directions (N = 16 unbaited traps), for the cerambycid species A) *Megacyllene caryae* (Friedman's $Q_{4,131} = 61.1$, $P < 0.0001$), and B) *Neoclytus acuminatus acuminatus* ($Q_{3,48} = 21.4$, $P < 0.0001$). Means with different letters within species are significantly different (Tukey's test, $P < 0.05$).



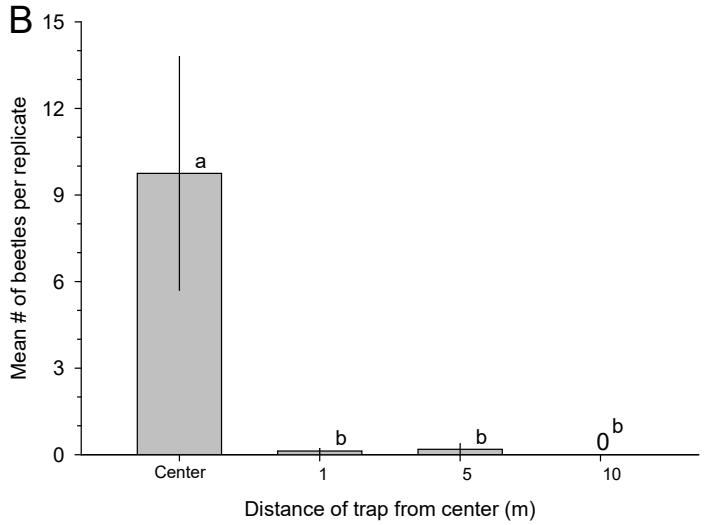


Fig. 3.2. Mean (± 1 SE) number of adults of *Xylotrechus colonus* that were caught during Experiment 3 by traps baited with *syn*- or *anti*-2,3-hexanediol (the test compounds, labeled *syn*- and *anti*-diol) versus unbaited control traps, in the presence and absence of traps baited with the strong attractant 3-hydroxyhexan-2one (labeled 3-ketol) (*syn*-diol: Friedman's $Q_{3,88} = 4.26$, $P = 0.0073$; *anti*-diol: $Q_{3,112} = 1.12$, $P > 0.05$). Data for the strong attractant were not included in the analysis.

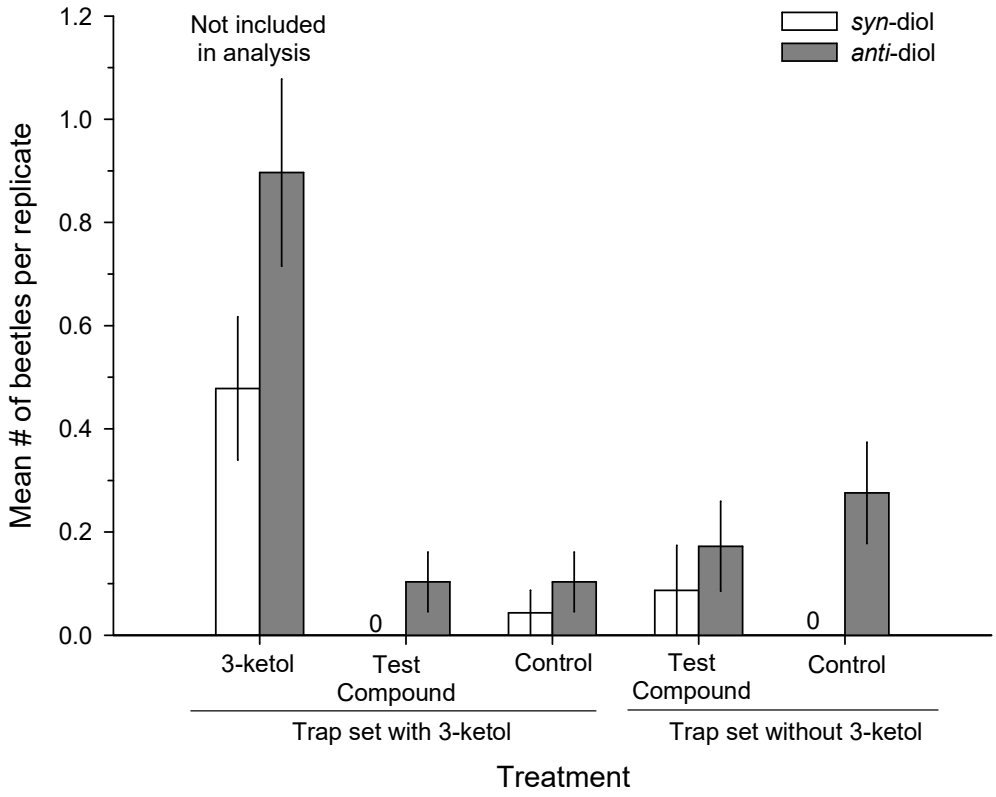


Fig. 3.3. Mean (± 1 SE) number of adults of *Neoclytus acuminatus acuminatus* that were caught during Experiment 3 by traps baited with the generic blend of all four stereoisomers of 2,3-hexanediol (the test compound) versus unbaited control traps, in the presence and absence of traps baited with the strong attractant *syn*-2,3-hexanediol (labeled *syn*-diol) (Friedman's $Q_{3,28}$ = 4.66, P = 0.0092). Data for the strong attractant were not included in the analysis.

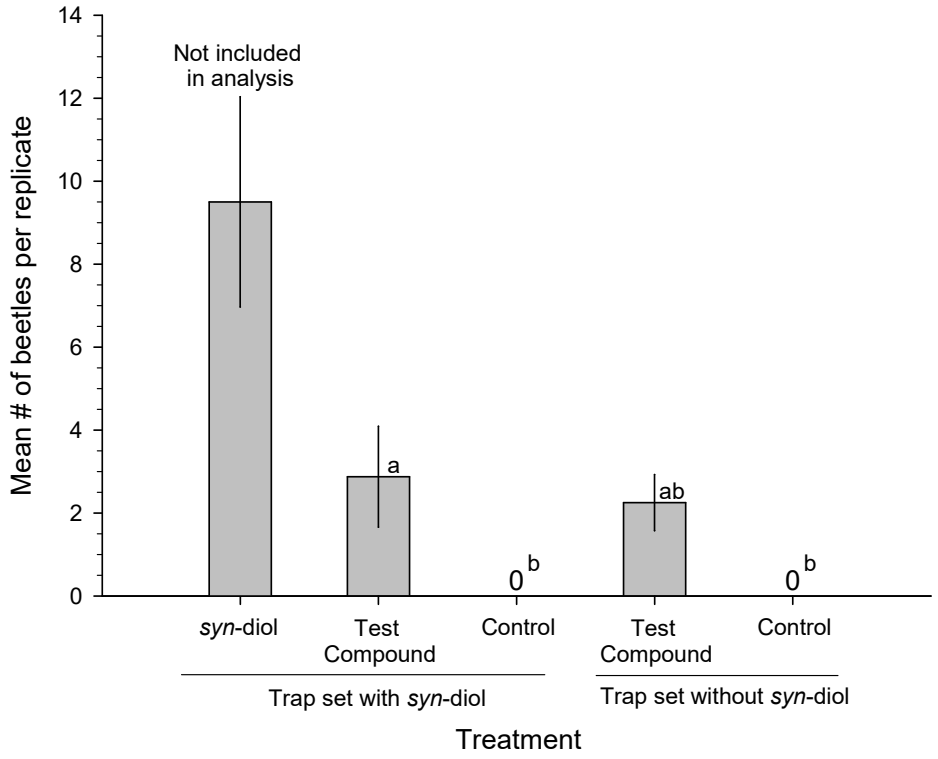


Fig. 3.4. Mean (± 1 SE) number of adult beetles captured during Experiment 4 by traps baited with varying concentrations of 3-hydroxyhexan-2-one for the cerambycid species: A) *Neoclytus mucronatus mucronatus* (Friedman's $Q_{5,258} = 5.49$, $P < 0.0001$), and B) *Xylotrechus colonus* ($Q_{5,258} = 4.80$, $P = 0.0003$).

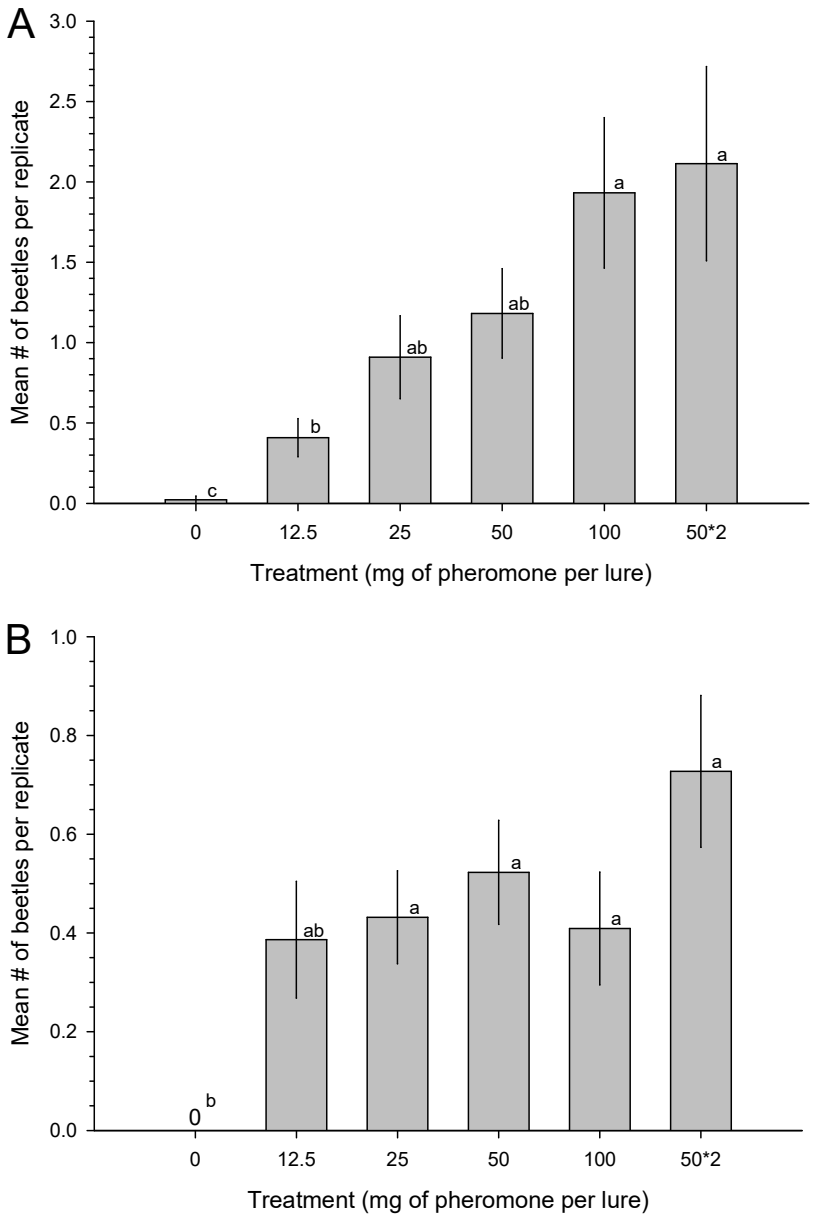


Fig. 3.5. Mean (± 1 SE) number of adults of *Xylotrechus colonus* that were captured by traps baited by varying concentrations of a blend of synthesized pheromones from multiple species of cerambycids (see text; Friedman's $Q_{4,55} = 3.35$, $P = 0.016$).

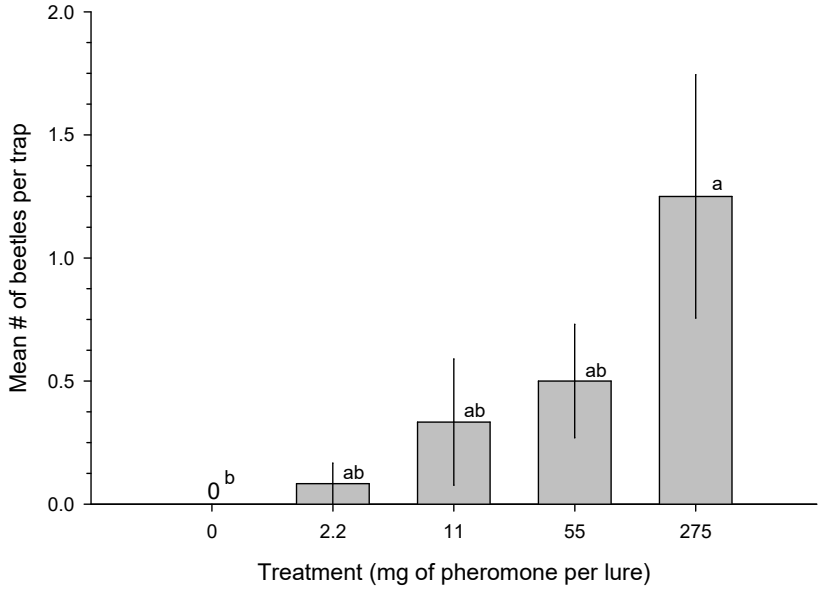
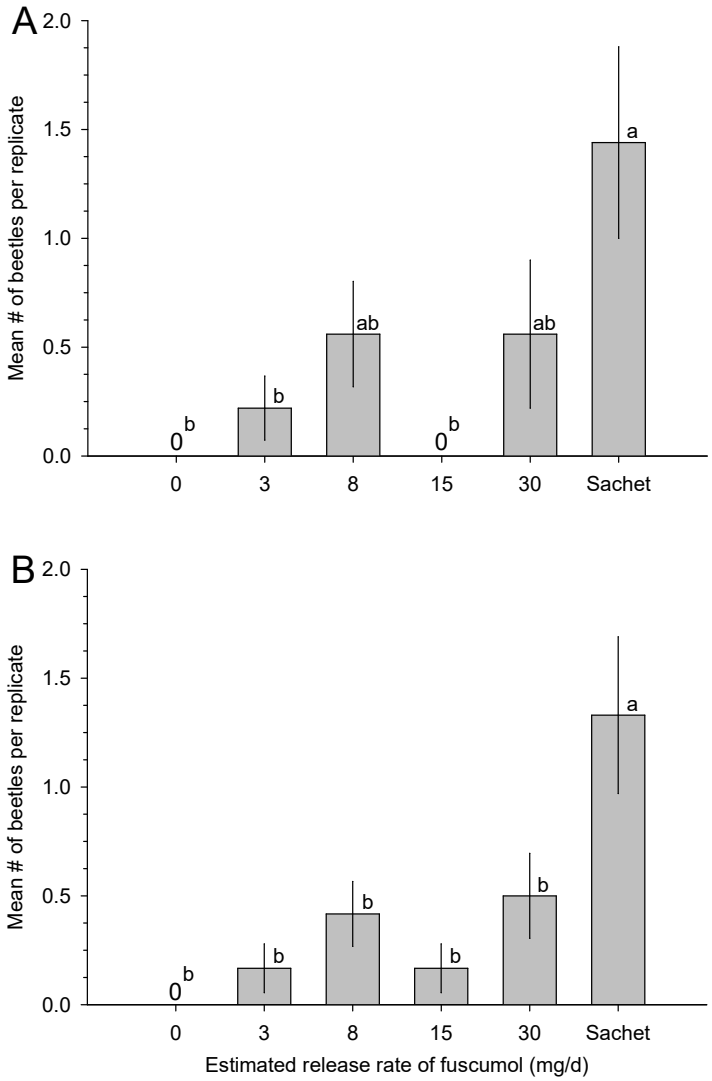


Fig. 3.6. Mean (± 1 SE) number of beetles captured by traps baited with emitters of varying release rates of fuscumol and fuscumol acetate for the cerambycid species: A) *Astylidius parvus* (Friedman's $Q_{5,48} = 4.49$, $P = 0.0019$), and B) *Lepturges angulatus* ($Q_{5,66} = 6.49$, $P < 0.0001$). "Sachet" lures were commercially available polyethylene bags with release rates of ~27 and 60 mg/d for fuscumol and fuscumol acetate, respectively.



CHAPTER 4: INFLUENCE OF VOLATILES FROM LARVAL HOST PLANTS ON ATTRACTION OF CERAMBYCID BEETLES TO SYNTHESIZED PHEROMONES

Abstract

Plant semiochemicals are known to have a wide range of effects on the behaviors of insects. Some insects produce or release sex pheromones in response to specific host plant cues, and volatiles from host plants often enhance response of insects to their pheromones. However, plant volatiles may also inhibit atrraction to these same pheromones or repel insects. Cerambycid beetles of many species are known to be strongly attracted by volatile chemicals produced by their host plants, some of which also enhanced attraction to aggregation pheromones produced by the male beetles. Most of the research on host plant volatiles has focused on species of cerambycids whose larvae develop in gymnosperms, and little is known of the chemicals that mediate location of host plants for species whose larvae develop in angiosperms. Here, we describe a field experiment which tested for attraction of cerambycid species to volatiles from angiosperm woody plants, and for enhancement of attraction to synthetized aggregation pheromones. The source of plant volatiles was chipped wood of five tree species which are natural hosts of cerambycid species native to the area of our studies (east-central Illinois). Traps caught 3,626 cerambycid beetles of 71 species in six subfamilies, and one species in the closely-related Disteniidae. The most numerous species were *Xylotrechus colonus* (F.) (34% of total) and *Neoclytus acuminatus acuminatus* (F.) (25%). Adults of many species were attracted to traps because their pheromone components were present in the blend, but no species were significantly attracted by plant volatiles alone. Nevertheless, species varied as to whether attraction to

pheromones was enhanced or inhibited by volatiles released from chipped wood of a particular tree species.

Introduction

Plant fragrances typically are made up of small, volatile organic molecules. These volatile plant compounds likely evolved to repel herbivores, but have been co-opted for a remarkable range of functions (Fraenkel 1959). Many species of insects locate their host plants by exploiting volatile chemicals that plants produce (Visser 1986, 1988). The process of host location is likely mediated by plant volatiles, as the proper host is often hidden amongst other plants that are not suitable. The recognition of a host plant through olfactory cues may occur by either recognition of specific compounds tied to a species of plant (Fraenkel 1959) or specific ratios of ubiquitous compounds (Visser 1986). Insects detect these volatiles through their antennae and, in some cases, their maxillary palps (de Bruyne et al. 1999) or labial palps (Kwon et al. 2006). The specialized cells on the surface of the antennae contain a receptor that recognizes and binds specific volatile compounds. This system is extremely sensitive, with some receptors being able to detect volatiles at extremely low concentrations (e.g., Buttery and Ling 1985, Liu et al. 1989).

It has long been known that adult cerambycid beetles of many species locate their host plants by olfaction (e.g., Beeson 1930), exploiting volatile chemicals that are released by the stressed or dying hosts which are required by their larvae, and floral volatiles from host plants of pollen-feeding adults (reviewed by Millar and Hanks 2016). Most of the research on plant kairomones of cerambycids has focused on species whose larvae develop in gymnosperms, and results have shown that volatiles from gymnosperms alone are effective in attracting the adults,

and also in enhancing attraction to the aggregation pheromones produced by males (e.g., Sweeney et al. 2004, Silk et al. 2007, Ryall et al. 2014). However, there has been little progress in identifying volatile attractants from angiosperm hosts of cerambycids, with much of the research limited to laboratory studies (e.g., Hanks et al. 1996, Ginzel and Hanks 2005, Fonseca et al. 2010).

The wood-boring larvae of many cerambycid species are important pests because they damage and kill their hosts, and also degrade the quality of trees felled for lumber (e.g., Solomon 1995). Some species also have become severe pests when introduced into new regions of the world by international commerce (Haack et al. 2010). There is a great need to develop effective methods of monitoring for new incursions by exotic and potentially invasive cerambycids, to manage native species which are pests, and to develop strategies for conserving native species which are endangered (e.g., Ray et al. 2014).

Here, we describe a field experiment which tested for attraction of cerambycid beetles to volatiles produced by angiosperm hosts, and enhancement of attraction to their synthesized pheromones. The experiments were conducted in wooded areas of east-central Illinois where there is a community of at least 90 native species of cerambycids whose larvae are known to develop in angiosperm hosts (Hanks et al. 2014; also see Lingafelter 2007).

Methods

Sources of chemicals.

Racemic 3-hydroxyhexan-2-one, 2-(undecyloxy)ethanol (termed monochamol), (*E*)-6,10-dimethylundeca-5,9-dien-2-ol (fuscumol), and (*E*)-6,10-dimethylundeca-5,9-dien-2-yl acetate (fuscumol acetate) were purchased from Bedoukian Research (Danbury, CN), and racemic 2-

methylbutan-1-ol from Sigma-Aldrich (St. Louis, MO). *Syn*-2,3-hexanediol was synthesized as described in Lacey et al. (2004).

Field bioassays.

Field bioassays were conducted at 15 study sites (Table 4.1), most of which were wooded with mature second-growth or successional hardwoods, and dominated by oak (*Quercus* species), hickory (*Carya* species), maple (*Acer* species), and ash (*Fraxinus* species). Five species of trees were chosen as the sources of volatiles, based on being native species and hosts for the cerambycid species that were common in the study area (see Hanks et al. 2014, Lingafelter 2007), including the angiosperms white oak (*Quercus alba* L.; Fagaceae), green ash (*Fraxinus pennsylvanica* Marshall; Oleaceae), black cherry (*Prunus serotina* Ehrh.; Rosaceae), black willow (*Salix nigra* Marshall; Salicaceae), and the gymnosperm eastern white pine (*Pinus strobus* L.; Pinaceae). Most of the cerambycid species native to the study area are polyphagous, with their larvae developing in a diversity of angiosperm hosts (see Yanega 1996, Lingafelter 2007).

Beetles were caught with panel traps (black cross-vane, AlphaScents, Portland, OR) that were coated with the fluoropolymer dispersion Fluon® PTFE (AGC Chemicals Americas, Inc., Exton, PA) to improve trapping efficiency (for details on trapping methods, see Graham et al. 2010). Traps were hung ~0.5 m above the ground from inverted L-shaped frames constructed of polyvinyl chloride pipe. Trap basins were partially filled with saturated aqueous NaCl solution as a killing agent and preservative. Pheromone lures contained a blend of synthesized pheromones of multiple cerambycid species which had been developed as a multi-species attractant (Hanks et al. 2012), including pheromones of species in the subfamily Cerambycinae (3-hydroxyhexan-2-

one, *syn*-2,3-hexanediol, 2-methylbutan-1-ol) and of species in the Lamiinae (fuscumol, fuscumol acetate, monochamol; reviewed by Millar and Hanks 2016). Pheromone lures consisted of polyethylene sachets (press-seal bags, Bagette model 14770, 5.1 × 7.6 cm, 0.05 mm thick, Cousin Corp., Largo, FL) loaded with 25 mg per enantiomer of each compound dissolved in 1 ml of isopropanol. Solvent control lures contained 1 ml of neat isopropanol.

The source of plant volatiles was chipped host material. Branches (2.5 - 5 cm maximum diameter) were cut from trees of the five tree species at the Trelease Woods, Vermilion River Observatory, and Nettie Hart Memorial Woods study sites (Table 4.1) during late March to early July 2012. Branches were chosen because a number of the targeted native species are known to attack branches, particularly larvae of the subfamilies Cerambycinae and the Lamiinae (Švácha and Lawrence 2014). The branches with bark intact were coarsely chipped with a power wood chipper (Earthquake model 212, Ardisam, Inc., Cumberland, WI) 1-2 d prior to setting up experiments. Traps were baited with 1 liter of wood chips in a cloth mesh bag that was hung in the central opening. Each species of tree in its own separate transect, with one transect per site. During early May 2012, one line transect of four traps (~10 m apart) were deployed at each of the 15 study sites, with the following treatments assigned to traps randomly: pheromone blend + wood chips, pheromone blend, solvent control lure + wood chips, solvent control lure only. Wood chips from the five tree species were tested independently, with tree species assigned randomly to study sites, and three transects of each tree species out at a particular time. Wood chip species were rotated through the different sites, in order to rotate each of the five tree species through all the sites, at the time of replacement. The experiment continued through early October 2012, the traps being serviced every ~1 wk, at which time treatments were rotated along

transects to control for positional effects. Wood chips were replaced with recently chipped wood (~1-2 d prior) every 4 weeks, at which time pheromone lures also were replaced.

Taxonomy of captured beetles follows Monné and Hovore (2005). Representative specimens of the cerambycid species represented in trap catch are available from the laboratory collection of LMH, and voucher specimens have been deposited at the Illinois Natural History Survey, Champaign, IL.

Statistical analysis.

The data were analyzed separately for the five tree species, including only the most numerous cerambycid species (at least 10 specimens), the replicates being defined by study site and collection date. No comparisons between tree species were made as the experimental design does not lend itself to testing differences between tree species because bioassays for the various tree species were not conducted at the same study sites at the same time. Differences between treatments in numbers of beetles caught per replicate were tested with the nonparametric Friedman's test (PROC FREQ with CMH option; SAS Institute 2011). The alpha level of the test was set at 0.01 in recognition of the number of analyses that were conducted. Replicates that captured no beetles of the focal species were dropped from analyses. This threshold of zero was increased for species that were caught in great numbers, so as to improve the robustness of the analysis while maintaining sufficient replication for good statistical power (at least 15 replicates). Pairs of treatment means were compared using the Ryan-Einot-Gabriel-Welsch *Q* (REGWQ) multiple comparison test, which controls for maximum experiment-wise error rates (SAS Institute 2011).

Results

During the experiment, traps caught a total of 3,626 cerambycid beetles of 71 species in six subfamilies, and one species in the closely-related Disteniidae (Table 4.2). The two most numerous species, together comprising ~60% of the specimens, were in the subfamily Cerambycinae: *Xylotrechus colonus* (F.) (34% of total) and *Neoclytus acuminatus acuminatus* (F.) (25%). The next most numerous species, each representing 3 to 8% of the total, were the cerambycines *Phymatodes lengi* Joutel and *Neoclytus mucronatus mucronatus* (F.), and three species in the subfamily Lamiinae: *Astyleiopus variegatus* (Haldeman), *Graphisurus fasciatus* (Degeer), and *Lepturges angulatus* (LeConte). Most of the remaining species were represented by few specimens, with 21 species (~30% of the total number) represented by only a single specimen (Table 4.2).

Twelve cerambycid species showed statistically significant overall treatment effects for the experiments that tested attraction to wood chips from the five tree species (Table 4.3). In most of the 32 cases present in Table 4.3, a case being a species of beetle and a particular tree species, for which the beetle species was captured in statistically relevant numbers, the beetles were significantly attracted to the pheromone blend. However, traps baited only with wood chips attracted very few beetles of any species, regardless of the species of tree, and never in numbers significantly different from control trap (Table 4.3). Wood chips clearly did not influence attraction of beetles to pheromones in about half the cases, with similar means for the pheromone + wood chips and pheromone alone treatments (18 of 32 cases, ~56%). In other cases, however, wood chips apparently enhanced attraction, or antagonized attraction to pheromones.

First, there were three cases in which beetles were significantly attracted by pheromone, but the mean for the pheromone + wood chips treatment was greater still (Table 4.3), suggesting

that volatiles from the chips enhanced attraction: willow chips for *N. a. acuminatus*, and oak chips for both *Phymatodes testaceus* (L.) and *G. fasciatus*. Further evidence that wood chips enhanced attraction was found in the five cases in which beetles were not significantly attracted by pheromones alone, but addition of wood chips resulted in a increase in attraction, including oak chips for *Anelaphus pumilus* (Newman), *Cyrtophorus verrucosus* (Oliver), *A. variegatus*, and *Sternidius alpha* (Say), willow chips for *X. colonus*, and pine chips for *L. angulatus*.

On the other hand, the presence of wood chips clearly antagonized attraction to pheromones in three cases, with the mean for the pheromone + wood chips treatment being significantly lower than that for the pheromone alone treatment: pine chips for *N. a. acuminatus*, ash chips for *A. variegatus*, and oak chips for *Astylidius parvus* (LeConte). Antagonism also was suggested in the two cases in which beetles were significantly attracted by pheromone, but the addition of wood chips resulted in a reduction in mean trap catch, including ash chips for *Elaphidion mucronatum* (Say), and pine chips for *G. fasciatus*.

Discussion

While we demonstrated that volatile chemicals released by angiosperm trees play an important role in host plant location by cerambycid beetles, the use of wood chips may not be simulating the correct state of a proper larval host. In this study, antagonism was brought on by plant volatiles, which suggests that these volatile chemicals released serve to steer cerambycids away from inappropriate hosts in addition to towards the location of an appropriate host. Our findings suggest that monitoring efforts for exotic or native species may be improved by using pheromones and appropriate larval host volatiles, provided that these host plants are known. Attraction of the 12 species of cerambycid beetles to traps baited with the blend of synthesized

pheromones was not surprising, because each of the species already was known to be attracted by the same pheromone blend from earlier studies, and for several species the blend was known to contain pheromone components (see Mitchell et al. 2011, Hanks et al. 2012, Hanks and Millar 2013, Handley et al. 2015, Meier et al. 2016). For example, 3-hydroxyhexan-2-one is the dominant or sole pheromone component, or at least a strong attractant, for the cerambycines *A. pumilus*, *C. verrucosus*, *N. m. mucronatus*, *P. testaceus*, and *X. colonus*. The pheromone of *N. a. acuminatus* is composed solely of (2*S*,3*S*)-2-3-hexanediol (Lacey et al. 2004), which was part of the *syn*-hexanediol component of the blend. Moreover, enantiomers of fuscumol and/or fuscumol acetate have been identified as pheromone components, or the racemic compounds are at least attractants, for all of the lamiine species which showed significant overall treatment effects (Table 4.3; Mitchell et al. 2011, Hanks and Millar 2013, Meier et al. 2016).

In many cases, the response of beetles to the presence of wood chips was consistent with what was known of their host plant associations (summarized in Linsley 1963, 1964; Linsley and Chemsak 1995; Lingafelter 2007; also see Chapter 2 of this dissertation). For example, oak chips enhanced attraction to pheromone for several species that are known to prefer oaks as larval hosts, including *A. pumilus*, *C. verrucosus*, *P. testaceus*, and *G. fasciatus*. Similarly, willow is among the preferred hosts of *N. a. acuminatus*, and willow chips enhanced attraction of adults of that species. In other cases, attraction was enhanced by chips from hosts which are at least within the host range of polyphagous species, such as willow chips for *X. colonus*, pine chips for *L. angulatus*, and pine chips for *S. alpha*.

Chips from trees of species that are not natural hosts, on the other hand, might be expected either to antagonize attraction to pheromone (if the species is under selection to avoid that tree species), or to have no effect on attraction (if the beetles are simply not adapted to detect

the characteristic volatile profile of that tree species). For example, pine chips antagonized attraction of *N. a. acuminatus* and *G. fasciatus*, both of which are limited to angiosperm hosts. Similarly, oak chips antagonized attraction of *A. parvus*, which, although it is an angiosperm generalist, is not known to use oaks as larval hosts. Evidence that beetles are not influenced by volatiles of non-hosts can be found in *N. m. mucronatus*, the larval hosts of which are limited primarily to hickories (*Carya* species), thus potentially explaining why adults of this species showed no response to chips from ash, cherry, or oak. Another such example is that of *A. variegatus*, adults of which apparently were not affected by pine chips, consistent with it only using angiosperm hosts.

Nevertheless, there are many findings from this study that remain unexplained. That is, most of the species in Table 4.3 are considered broadly polyphagous, yet many species appeared unaffected by wood chips of likely hosts, particularly *N. a. acuminatus*, *X. colonus*, *G. fasciatus*, and *L. angulatus*. Adults of *X. colonus* already were shown to be attracted by volatiles from larval hosts in laboratory experiments (Ginzel and Hanks 2005). In a study parallel to the present study which was conducted in California, Collignon et al. (2016) also found that chipped oak wood failed to enhance attraction to the same blend of synthesized pheromones for four species of cerambycids whose larvae develop in oaks, nor were beetles attracted to traps baited with oak chips alone. Chips from a non-host conifer, however, antagonized attraction of one species in that study.

The lack of a wood chip effect for cerambycid beetles in both the present study and that of Collignon et al. (2016) may be due to the limitations of the experimental design. The relatively small amounts of host material that were used (i.e., 1 liter of chipped wood) would have yielded small quantities of volatiles compared to what would be produced by larval hosts in

the vicinity of the traps. Moreover, these host materials originated from branches of living trees, which may not have been representative of the host condition required by the larvae. That is, many of the species in Table 3 require hosts that are moribund or dead, and volatile profiles from such hosts undoubtedly differ from those produced by chipped wood from living hosts. In that case, plant volatiles may be indicative of an inappropriate host, and so would antagonize attraction. Such might be the case of *E. mucronatum*, the larvae of which develop in seasoned dead wood (Linsley 1963), which may account for the antagonistic effect that freshly chipped ash had on attraction to the pheromone blend.

In summary, this study provides further evidence that volatile chemicals released by angiosperm trees play an important role in host plant location by cerambycid beetles, perhaps by associating production of aggregation pheromone with presence of a suitable larval host. Antagonism by plant volatiles further suggests that host location is guided not only by attractants from suitable hosts, but also by chemicals which serve to repel beetles from inappropriate hosts. From a practical standpoint, these findings suggest that methods of trapping cerambycids, such as in monitoring to detect introductions of exotic species, or for developing methods of conserving endangered species, may be improved by baiting traps with both synthesized pheromones and the appropriate host plant volatiles.

Acknowledgments

We thank Linnea Meier, Peter Reagel, and Joy Wernz for assistance in the field. This project was supported by funding from The Alphawood Foundation of Chicago (to Lawrence M. Hanks) and the USDA National Institute of Food and Agriculture, grant number # 2012-67013-19303 (to Jocelyn G. Millar and LMH).

References

Beeson, C.F.C. 1930. Sense of smell of longicorn beetles. Nature 126: 12.

Buttery, R. G., and L. C. Ling. 1985. Volatile components of corn roots: Possible insect attractants. J. Agr. Food Chem. 33: 772–774.

Collignon, M. R., I. Swift, Y. Zou, J. S. McElfresh, L. M. Hanks, J. G. Millar. 2016. The influence of host plant volatiles on the attraction of longhorned beetles (Coleoptera: Cerambycidae) to pheromones. J. Chem. Ecol. (in press).

De Bruyne, M., P. J. Clyne, and J. R. Carlson. 1999. Odor coding in a model olfactory organ: the *Drosophila* maxillary palp. J. Neurosci. 19: 4520–4532.

Fonseca M. G. , D. M. Vidal, and P. H. G. Zarbin. 2010. Male-produced sex pheromone of the cerambycid beetle *Hedypathes betulinus*: chemical identification and biological activity. J. Chem. Ecol. 36:1132–1139.

Fraenkel, G. S. 1959. The raison d'etre of secondary plant substances. Science 129: 1466–1470.

Ginzel, M. D., and L. M. Hanks. 2005. Role of host plant volatiles in mate location for three species of longhorned beetles. J. Chem. Ecol. 31: 213–217.

Graham, E. E., R. F. Mitchell, P. F. Reagel, J. D. Barbour, J. G. Millar, and L. M. Hanks. 2010. Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles. J. Econ. Entomol. 103: 641–647.

Haack R. A., F. Hérard, J. Sun, and J. J. Turgeon. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: A worldwide perspective. Annu. Rev. Entomol. 55: 521–546.

Handley, K., J. Hough-Goldstein, L. M. Hanks, J. G. Millar, and V. D'Amico. 2015. Species richness and phenology of cerambycid beetles in urban forest fragments of northern Delaware. Ann. Entomol. Soc. Am. 108: 251–262.

Hanks, L. M., and J. G. Millar. 2013. Field bioassays of cerambycid pheromones reveal widespread parsimony of pheromone structures, enhancement by host plant volatiles, and antagonism by components from heterospecifics. Chemoecology 23: 21–44.

Hanks, L. M., J. G. Millar, and T. D. Paine. 1996. Mating behavior of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) and the adaptive significance of long "horns". J. Insect Behav. 9: 383–393.

Hanks, L. M., J. G. Millar, J. A. Mongold-Diers, J.C.H. Wong, L. R. Meier, P. F. Reagel, and R. F. Mitchell. 2012. Using blends of cerambycid beetle pheromones and host plant volatiles to simultaneously attract a diversity of cerambycid species. Can. J. For. Res. 42: 1050–1059.

Hanks, L. M., P. F. Reagel, R. F. Mitchell, J.C.H. Wong, L. R. Meier, C. A. Silliman, E. E. Graham, B. L. Striman, K. P. Robinson, J. A. Mongold-Diers, and J. G. Millar. 2014. Seasonal phenology of the cerambycid beetles of east-central Illinois. Ann. Entomol. Soc. Am. 107: 211–226.

Kwon, H. W., M. Rutzler, and L. J. Zwiebel. 2006. Olfactory responses in a gustatory organ of the malaria vector mosquito *Anopheles gambiae*. Proc. Natl. Acad. Sci. USA 103: 13526–13531.

Lacey, E. S., M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2004. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus acuminatus acuminatus*. J. Chem. Ecol. 30: 1493–1507.

Lingafelter S. W. 2007. Illustrated key to the longhorned wood-boring beetles of the eastern United States. Coleopterists Society, North Potomac, MD.

Linsley, E. G. 1963. The Cerambycidae of North America, Part IV. Taxonomy and classification of the subfamily Cerambycinae, tribes Elaphidionini through Rhinotragini. University of California Publications in Entomology 21. University of California Press, Berkeley, CA.

Linsley, E. G. 1964. The Cerambycidae of North America, Part V. Taxonomy and classification of the subfamily Cerambycinae, tribes Callichromini through Ancylocerini. University of California Press, Berkeley, CA.

Linsley, E. G., and J. A. Chemsak. 1995. The Cerambycidae of North America, Part VII, No. 2: Taxonomy and classification of the subfamily Lamiinae, tribes Acanthocinini through Hemilophini. University of California Press, Berkeley, CA.

Liu, S. H., D. M. Norris, and P. Lyne. 1989. Volatiles from the foliage of soybean, *Glycine max*, and lima bean, *Phaseolus lunatus*: their behavioral effects on the insects *Trichoplusia ni* and *Epilachna varivestis*. J. Agr. Food Chem. 37: 496–501.

Meier, L. R., Y. Zou, J. G. Millar, J. A. Mongold-Diers, and L. M. Hanks. 2016. Synergism between enantiomers creates species-specific pheromone blends and minimizes cross-attraction for two species of cerambycid beetles. J. Chem. Ecol. (in press).

Millar, J. G., and L. M. Hanks. 2016. Chemical ecology of cerambycid beetles. *In* Q. Wang (ed.) Cerambycidae of the world: biology and pest management. CRC Press/Taylor & Francis, Boca Raton, FL. (in press).

Mitchell, R. F., E. E. Graham, J.C.H. Wong, P. F. Reagel, B. L. Striman, G. P. Hughes, M. A. Paschen, M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2011. Fuscumol and fuscumol

acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. Entomol. Exp. Appl. 141: 71–77.

Monné, M. A., and F. T. Hovore. 2005. Checklist of the Cerambycidae (Coleoptera) of the Western Hemisphere. BioQuip, Rancho Dominguez, CA.

Ray, A. M., R. A. Arnold, I. Swift, P. A. Schapker, S. McCann, C. J. Marshall, J. S. McElfresh, and J. G. Millar. 2014. (*R*)-desmolactone is a sex pheromone or attractant for the endangered valley elderberry longhorn beetle *Desmocerus californicus dimorphus* and several congeners (Cerambycidae: Lepturinae). PLoS One 9: e115498.

Ryall K., P. J. Silk, R. P. Webster, J. M. Gutowski, Q. Meng, Y. Li, W. Gao, J. Fidgen, T. Kimoto, T. Scarr, V. Mastro, and J. D. Sweeney. 2014. Further evidence that monochamol is attractive to Monochamus (Coleoptera: Cerambycidae) species, with attraction synergised by host plant volatiles and bark beetle (Coleoptera: Curculionidae) pheromones. Can. Entomol. 147: 564–579.

SAS Institute. 2011. SAS/STAT User's Guide release 9.3. SAS Institute, Cary, NC.

Silk, P. J., J. Sweeney, J. Wu, J. Price, J.M. Gutowski, and E. G. Kettela. 2007. Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). Naturwissenschaften 94: 697–701.

Solomon, J. D. 1995. Agriculture Handbook 706, guide to insect borers of North American broadleaf trees and shrubs. USDA Forest Service, Washington, DC.

Sweeney J. D., P. De Groot, L. MacDonald, S. Smith, C. Cocquempot, M. Kenis, and J. M. Gutowski. 2004. Host volatile attractants and traps for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* L., and other longhorned beetles (Coleoptera: Cerambycidae). Environ. Entomol. 33: 844–854.

Švácha, P., and J. F. Lawrence. 2014. Chapter 2.4 Cerambycidae Latreille, 1802, pp. 77–177. In R.A.B. Leschen and R. G. Beutel (eds.) Handbook of zoology: Arthropoda: Insecta: Coleoptera, beetles. Vol. 3: Morphology and systematics (Phytophaga). Walter de Gruyter, Berlin/Boston.

Visser, J. H. 1986. Host odor perception in phytophagous insects. Annu. Rev. Entomol. 31: 121–144.

Visser, J. H. 1988. Host-plant finding by insects: orientation, sensory input and search patterns. J. Insect Physiol. 34: 259–268.

Yanega D. 1996. Manual 6, field guide to northeastern longhorned beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey, Champaign, IL.

Tables

Table 4.1. Study sites for the field experiment conducted in central Illinois during 2012.

County/Name	**GPS coordinates (lat., long.)**	**Area (ha)**
Champaign		
Brownfield Woods[a]	40.144, -88.165	26
CCDC Collins Woods[a]	39.883, -88.178	6
Homer Lake Forest Preserve[b]	40.061, -87.987	330
Lake of the Woods Preserve[b]	40.204, -88.375	135
Middle Fork River Forest Preserve[b]	40.398, -87.991	890
Nanney Research Area[a]	40.138, -88.037	18
Nettie Hart Memorial Woods[a]	40.229, -88.358	16
Phillips Tract[a]	40.130, -88.150	52
Trelease Woods[a]	40.132, -88.141	29
McLean		
Funk Forest[a]	40.357, -89.127	25
Piatt		
Robert Allerton Park[a]	39.996, -88.651	600
Vermilion		
Edgar and Sophia Richter Research Area[a]	40.089, -87.811	9
Forest Glen Preserve[c]	40.019, -87.567	3
Rutan Research Area[a]	40.073, -87.907	10
Vermilion River Observatory[a]	40.058, -87.566	192

[a] University of Illinois (http://research.illinois.edu/cna/).

[b] Champaign County Forest Preserves district, Illinois (http://www.ccfpd.org).

[c] Vermilion County Conservation District (http://www.vccd.org/).

Table 4.2. Number of adult cerambycid beetles trapped during the field experiment which tested the effect of wood chips on attraction to synthesized pheromones, and the species of tree that were the sources of wood chips. Tree species: "ash" (green ash, *Fraxinus pennsylvanica* Marshall; Oleaceae), "cherry" (black cherry, *Prunus serotina* Ehrh.; Rosaceae), "oak" (white oak, *Quercus alba* L.; Fagaceae), "willow" (black willow, *Salix nigra* Marshall; Salicaceae), "pine" (eastern white pine, *Pinus strobus* L.; Pinaceae).

Taxonomy	**Ash**	**Cherry**	**Oak**	**Willow**	**Pine**	**Total**
Cerambycinae						
Anaglyptini						
Cyrtophorus verrucosus (Olivier)	11		32	2		45
Callidiini						
Phymatodes aereus (Newman)			3			3
Phymatodes amoenus (Say)	1	2	10			13
Phymatodes lengi Joutel	23	104	11	8		146
Phymatodes testaceus (L.)			36			36
Phymatodes varius (F.)			2			2
Clytini						
Megacyllene caryae (Gahan)			1			1
Neoclytus a. acuminatus (F.)	336	117	317	86	51	907
Neoclytus caprea (Say)			1			1
Neoclytus jouteli Davis		1				1
Neoclytus m. mucronatus (F.)	43	34	62	10	4	153
Neoclytus scutellaris (Olivier)	2		1	1	1	5
Sarosesthes fulminans (F.)	4		3			7
Xylotrechus colonus (F.)	508	195	335	68	115	1,221
Xylotrechus convergens LeConte		4				4
Curiini						
Curius dentatus Newman				1		1

Table 4.2 (cont.).

Taxonomy	Ash	Cherry	Oak	Willow	Pine	Total
Dryobiini						
Dryobius sexnotatus Linsley	1					1
Eburiini						
Eburia quadrigeminata (Say)	1	1	1			3
Elaphidiini						
Anelaphus parallelus (Newman)					1	1
Anelaphus pumilus (Newman)	19		32			51
Anelaphus villosus (F.)		1				1
Elaphidion mucronatum (Say)	24	10	22		9	65
Enaphalodes atomarius (Drury)	2					2
Micranoplium unicolor (Haldeman)			1			1
Parelaphidion aspersum (Haldeman)	5	2	6		1	14
Parelaphidion incertum (Newman)	2		1			3
Hesperophanini						
Tylonotus bimaculatus Haldeman	1					1
Neoibidionini						
Heterachthes quadrimaculatus Haldeman	1		1			2
Obriini						
Obrium maculatum (Olivier)		1				1
Smodicini						
Smodicum cucujiforme (Say)		1				1
Tillomorphini						
Euderces picipes (F.)		1	1	1		3
Lamiinae						
Acanthocinini						
Astyleiopus variegatus (Haldeman)	28	20	37	9	13	107
Astylidius parvus (LeConte)	10	12	18	2	8	57
Astylopsis macula (Say)	10	12	9		2	33

Table 4.2 (cont.).

Taxonomy	Ash	Cherry	Oak	Willow	Pine	Total
Graphisurus despectus (LeConte)	9	3	4			16
Graphisurus fasciatus (Degeer)	92	45	61	26	56	280
Hyperplatys maculata Haldeman	1	1	1			3
Leptostylus transversus (Gyllenhal)	6	5	13	4	2	30
Lepturges angulatus (LeConte)	56	18	44	7	2	127
Lepturges confluens (Haldeman)	5	3	1		4	13
Lepturges regularis (LeConte)	1		19		5	25
Lepturges symmetricus (Haldeman)	2				1	3
Sternidius alpha (Say)	23	8	14	10	156	211
Sternidius misellus (LeConte)	2	2				4
Urgleptes querci (Fitch)	2	3	1	1		7
Urgleptes signatus (LeConte)	1		2			3
Acanthoderini						
Aegomorphus modestus (Gyllenhal)	9	13	8		5	35
Oplosia nubila (LeConte)			2			2
Desmiphorini						
Eupogonius pauper LeConte	1					1
Psenocerus supernotatus (Say)	3	1	1	2		7
Dorcaschematini						
Dorcaschema alternatum (Say)		1			1	2
Dorcaschema cinereum (Olivier)	1	1			1	3
Oberiini						
Oberea perspicillata Haldeman			1			1
Pogonocherini						
Ecyrus d. dasycerus (Say)	2		2			4
Saperdini						
Saperda discoidea F.	1	2	2			5
Saperda imitans Felt and Joutel	6	3	6	1		16

Table 4.2 (cont.).

Taxonomy	Ash	Cherry	Oak	Willow	Pine	Total
Saperda lateralis F.					1	1
Saperda puncticollis Say	1					1
Saperda vestita Say	1		1			2
Lepturinae						
Lepturini						
Bellamira scalaris (Say)	1					1
Brachyleptura rubrica (Say)		1				1
Strangalia famelica Newman		1				1
Typocerus lugubris (Say)				1		1
Typocerus velutina (Olivier)					2	2
Rhagiini						
Gaurotes cyanipennis (Say)	7	2	3			12
Stenocorus cinnamopterus (Randall)			1			1
Necydalinae						
Necydalis mellita (Say)		2		1		3
Parandrinae						
Parandrini						
Neandra brunnea (F.)	7	6	29		1	43
Prioninae						
Prionini						
Orthosoma brunneum (Forster)	6	1	4		1	12
Disteniidae						
Disteniini						
Elytrimitatrix undata (F.)	3					3
	1,289	639	1,164	241	293	3,626

Table 4.3. Mean (± 1 SE) number of cerambycid beetles captured per treatment, and results of Friedman's *Q* analysis, for the cases in which overall treatment effects were statistically significant. "Tree species" (as defined in Table 2) indicates the sources of wood chips. Asterisks indicate significance level of Friedman's *Q*: * $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$. Means with different letters within species are significantly different (REGWQ test, $P < 0.05$). Bold font indicates means that are statistically greater than all other treatment means.

Taxonomy	Tree species	Pheromone + wood chips	Pheromone	Wood chips	Control	Friedman's *Q* (df)
Cerambycinae						
Anelaphus pumilus	Oak	2.4 ± 0.8a	1.7 ± 0.7ab	0b	0b	15.0 (32)*
Cyrtophorus verrucosus	Oak	1.6 ± 0.5a	0.80 ± 0.2ab	0.5 ± 0.2b	0.3 ± 0.2b	9.7 (40)*
Elaphidion mucronatum	Ash	0.86 ± 0.4ab	2.4 ± 0.8a	0b	0.14 ± 0.1b	12.2 (28)*
	Oak	1.0 ± 0.2a	0.75 ± 0.3a	0.08 ± 0.08b	0b	18.1 (48)**
Neoclytus a. acuminatus	Ash	5.2 ± 1.3a	7.3 ± 1.0a	0b	0b	56.5 (90)***
	Cherry	2.7 ± 0.6a	3.3 ± 0.8a	0.30± 0.2b	0b	31.0 (69)***
	Oak	5.9 ± 0.6a	7.8 ± 2.4a	0b	0.27 ± 0.1b	40.0 (60) ***
	Willow	**3.9 ± 0.8a**	2.0 ± 0.3b	0c	0c	33.8 (52)***
	Pine	1.0 ± 0.3b	**3.1 ± 1.2a**	0.08 ± 0.08b	0.08 ± 0.08b	21.7 (48)***

Table 4.3 (cont.).

Taxonomy	Tree species	Pheromone + wood chips	Pheromone	Wood chips	Control	Friedman's *Q* (df)
Neoclytus m. mucronatus	Ash	0.85 ± 0.2a	1.3 ± 0.3a	0b	0b	30.0 (79)***
	Cherry	1.1 ± 0.4a	1.3 ± 0.6a	0b	0.1 ± 0.1b	13.1 (55)*
	Oak	1.0 ± 0.3a	1.8 ± 0.3a	0.10 ± 0.07b	0b	34.2 (86)***
Phymatodes testaceus	Oak	**4.5 ± 1.4a**	1.3 ± 0.8b	0.17 ± 0.17b	0b	12.3 (24)*
Xylotrechus colonus	Ash	10.6 ± 2.2a	14.2 ± 3.4a	0.46 ± 0.3b	0.27 ± 0.2b	40.7 (62)***
	Cherry	4.3 ± 1.4a	5.2 ± 2.3a	0.05 ± 0.05b	0.26 ± 0.1b	34.1 (78)***
	Oak	8.2 ± 1.1a	6.4 ± 2.2a	0.5 ± 0.3b	0.21 ± 0.2b	32.4 (56)***
	Willow	2.6 ± 1.1a	1.5 ± 0.5ab	0.2 ± 0.1b	0.27 ± 0.1b	17.6 (60)**
	Pine	3.9 ± 1.2a	3.6 ± 1.2a	0.36 ± 0.2b	0.36 ± 0.1b	16.4 (56)**
Lamiinae						
Astyleiopus variegatus	Ash	0.56 ± 0.2b	**1.2 ± 0.28a**	0c	0.06 ± 0.06bc	20.6 (63) ***
	Oak	1.4 ± 0.2a	0.82 ± 0.3ab	0.09 ± 0.09b	0.09 ± 0.09b	16.4 (44)**
	Pine	1.0 ± 0.2a	0.86 ± 0.3a	0b	0b	14.8 (28)*
Astylidius parvus	Oak	0.50 ± 0.2b	**0.92 ± 0.2a**	0.08 ± 0.08c	0c	17.8 (48)**
Graphisurus fasciatus	Ash	2.5 ± 0.6a	2.0 ± 0.5a	0.25 ± 0.1b	0.42 ± 0.3b	35.1 (80)***
	Cherry	1.5 ± 0.4a	1.6 ± 0.5a	0.2 ± 0.1b	0.4 ± 0.2b	11.4 (48)*
	Oak	**2.1 ± 0.6a**	1.1 ± 0.3b	0.06 ± 0.06b	0.17 ± 0.1b	25.0 (72)***
	Willow	2.3 ± 0.8a	1.8 ± 0.9a	0b	0.17 ± 0.17b	14.7 (24)*
	Pine	2.6 ± 0.8ab	3.9 ± 1.4a	0.13 ± 0.1b	0.38 ± 0.23b	15.8 (32)*

Table 4.3 (cont.).

Taxonomy	Tree species	Pheromone + wood chips	Pheromone	Wood chips	Control	Friedman's *Q* (df)
Lepturges angulatus	Ash	1.4 ± 0.25a	1.5 ± 0.4a	0b	0b	34.3 (79)***
	Oak	1.5 ± 0.4a	1.7 ± 0.6a	0b	0b	16.0 (39)*
	Pine	3.2 ± 1a	2.2 ± 0.7ab	0b	0b	12.5 (20)*
Sternidius alpha	Ash	1.2 ± 0.2a	1.1 ± 0.3a	0b	0b	20.8 (40)***
	Oak	0.89 ± 0.3a	0.67 ± 0.2ab	0b	0b	12.1 (35)*

CHAPTER 5: INFLUENCE OF FERMENTING BAIT AND VERTICAL POSITION OF TRAPS ON ATTRACTION OF CERAMBYCID BEETLES TO PHEROMONE LURES

Abstract

Many researchers have attempted to improve methods of trapping wood-boring beetles by developing more effective designs for pheromone-baited traps. However, information on the effectiveness of alternative types of baits, such as fermenting baits which produce volatiles that are known to attract some species of cerambycids, is often scattered and anecdotal, rather than being the result of comparative studies of different bait types. Here, we describe a field experiment in east-central Illinois which tested whether attraction of beetles to a blend of synthesized cerambycid pheromones would be enhanced by volatiles from fermenting bait composed of crushed fruit, sugars, yeast, and wood chips. A second experiment tested the same treatments, but also assessed how trap catch was influenced by the vertical position of traps within forests (understory versus within the canopy). During the two experiments, 885 cerambycid beetles of 37 species were caught, with *Xylotrechus colonus* (F.) (subfamily Cerambycinae) captured in greatest numbers (~52% of total). Adults of several cerambycid species were significantly attracted by the pheromone blend, but *X. colonus* and *Graphisurus fasciatus* (Degeer) (subfamily Lamiinae) were the only species for which attraction was significantly enhanced by the fermenting bait. Traps in the forest understory captured the greatest number of *X. colonus* and *G. fasciatus*, whereas more adults of the cerambycine *Neoclytus m. mucronatus* (F.) were captured in the forest canopy rather than the understory.

Introduction

Wood-boring beetles in the Cerambycidae play important roles in forest ecosystems, especially as nutrient recyclers which initiate the breakdown of dead woody plants (Linsley 1959). Because the larvae feed within woody plants, they are difficult to detect, and are readily transported in lumber and other wooden products. As a result, increasing numbers of exotic cerambycid species are being introduced into new regions of the world through international commerce, and many of these species pose a threat to woody plants in natural and managed forests (Nowak et al. 2001, Brockerhoff et al. 2006). Effective methods for detecting exotic and potentially invasive cerambycid species, and for monitoring native species for conservation purposes (e.g., Ray et al. 2014) would form valuable tools for forest managers and regulatory personnel.

Over the past decade, there has been a great deal of progress in identifying pheromones of cerambycid beetles for use as lures in traps (reviewed by Millar and Hanks 2016). Blends of the synthesized pheromones of several species have been developed as multi-species lures that are broadly attractive to multiple species (e.g., Hanks et al. 2012). In parallel with this pheromone work, more effective traps have been developed (e.g., Bouget et al. 2008, Miller and Crowe 2009, Allison et al. 2014, Álvarez et al. 2014, Dodds et al. 2015), that have been rendered even more efficient in capturing and retaining beetles by coating their surfaces with lubricants (e.g., Graham et al. 2010, Allison et al. 2011, Álvarez et al. 2014). Furthermore, several studies have shown that the vertical position of traps within forests can be important for comprehensive assessment of cerambycid communities, because adults of some species appear to be localized within specific vertical strata of forests (e.g., Vance et al. 2003, Wermelinger et al. 2007, Graham et al. 2012).

Many species of cerambycids are known to be attracted by volatiles emitted by the host plants of their larvae (reviewed by Hanks and Wang 2016). Synthetic reconstructions of host volatiles enhanced attraction of some cerambycid species to their pheromones, increasing the diversity and number of beetles attracted to traps by pheromone lures (e.g., Sweeney et al. 2004, Silk et al. 2007, Hanks et al. 2012). Scattered reports extending over a number of decades suggest that fermenting baits, consisting of aqueous blends of sugary substances and alcoholic beverages which are allowed to ferment, produce volatiles that attract some species of wood-boring insects (Champlain and Knull 1932, Linsley 1959, Galford 1980). These baits constitute another possible source of attractants for some wood-boring insects, including cerambycids.

In an earlier study, Schmeelk et al. (2016) compared attraction of cerambycid beetles to traps baited with either a blend of synthesized pheromones or a fermenting bait in forests of east-central Illinois. Traps were positioned at three heights within forests. They found that pheromone-baited traps captured greater numbers of beetles than did traps baited with the fermenting bait. Captures were stratified, with some species being captured in greater numbers by traps in the understory, whereas others were more numerous in traps in the forest canopy. Here, we describe follow-up experiments which tested whether fermentation volatiles might enhance attraction to a pheromone blend, at one of the same field sites used by Schmeelk et al. (2016), and also tested the effect of trap height by positioning traps either in the forest understory or at mid-canopy height.

Materials and Methods

Field bioassays.

Research was conducted at Forest Glen Preserve (Vermilion Co. Conservation District, http://www.vccd.org/; 40.015°N, -87.568°W), a 3-ha secondary forest dominated by oaks (*Quercus* species), hickories (*Carya* species), maples (*Acer* species), and ash (*Fraxinus* species). Beetles were captured with panel traps (cross-vane, black corrugated plastic; AlphaScents, Portland, OR) that were coated with the fluoropolymer dispersion Fluon® PTFE (AGC Chemicals Americas, Inc., Exton, PA) to enhance trapping efficiency (for details, see Graham et al. 2010). Trap basins were partially filled with saturated aqueous NaCl solution as a killing agent and preservative.

Traps were baited with either a blend of synthetized pheromones of cerambycids or a fermenting bait. The pheromone treatment comprised a blend of pheromones of diverse species that had been developed as a multi-species lure (Hanks et al. 2012), including pheromones of species in the subfamily Cerambycinae (racemic 3-hydroxyhexan-2-one, *syn*-2,3-hexanediol, racemic 2-methylbutan-1-ol) and of species in the Lamiinae ([*E*]-fuscumol, [*E*]-fuscumol acetate, monochamol; reviewed by Millar and Hanks 2016). Lures were formulated to contain 25 mg of each pheromone enantiomer (i.e., 50 mg of racemic compounds) dissolved in 1 ml of isopropanol. Control lures contained 1 ml of neat isopropanol. Pheromone emitters were transparent polyethylene sachets (press-seal bags, Bagette model 14770, 5.1 × 7.6 cm, 0.05 mm thick, Cousin Corp., Largo, FL) which contained a cotton roll (1 × 4 cm dental wick, Patterson Dental Supply, Inc., St. Paul, MN). The recipe for the fermenting bait was based on the methods of Galford (1980), as follows: crushed banana (0.45 kg), brown sugar (0.45 kg), molasses (20 ml), baker's yeast (7 g), and coarsely chipped hickory wood (1.5 liter; Full Circle™ smoking

wood for barbecue, Topco Associates LLC, Elk Grove, IL) were added to 3 liters of water and allowed to ferment under ambient laboratory conditions (~23 ^{o}C) for 3 d. Lures consisted of 200 ml of the resulting liquid in polyethylene sachets (10 × 15 cm, 0.05 mm thick, Bagette model 14772, Cousin Corp.) with four holes (~5.5 mm) punched below the seal to increase release rate of volatiles.

Experiment 1 compared attraction of beetles to the pheromone blend, fermenting bait, and the two lure types combined using traps deployed 10 m apart in two separate linear transects (~15 m apart) in the forest understory. Traps were mounted on inverted L-shaped frames constructed of polyvinyl chloride (PVC) pipe (bottom of panels ~1 m above the ground). Treatments were as follows: 1) pheromone blend + fermenting bait (separate lures), 2) pheromone blend, 3) fermenting bait, and 4) solvent control. The experiment was conducted from 23 June to 11 September 2015, treatments were randomly assigned to traps within transects on the day of setup. Traps were serviced at intervals of ~2 d, at which time treatments were rotated one position along transects to control for positional effects.

Experiment 2 also tested the attraction of beetles to the pheromone blend, fermenting bait, and the combination, but included a trap height treatment. Panel traps of the same type were deployed in pairs such that one trap was mounted on a PVC frame in the understory (as already described), and above it a trap was suspended from the branch in the mid-canopy (~12 m above the ground) of a sugar maple (*Acer saccharum* Marsh.). Traps in the mid-canopy were positioned by first throwing a line over the branch with a large slingshot (Big Shot®, Sherrill Inc., Greensboro, NC), then hauling the trap up to that height, following the methods of Hughes et al. (2014). Sugar maples were chosen for this treatment because the mid-canopy branches tended to be more nearly horizontal than trees of other species, and so more suitable for suspending traps.

One transect was set out, with a total of eight traps, four traps were hung from the mid-canopy branches and four traps were placed directly beneath each of the four mid-canopy traps, with each pair of traps (understory and mid-canopy) receiving the same treatment. The experiment was conducted from 16 July to 11 September 2015, and traps were serviced at intervals of ~2 d, at which time treatments (per pair of traps) were rotated along transects.

Taxonomy of captured beetles follows Monné and Hovore (2005). Representative specimens of all species are available from the laboratory of LMH, and vouchers have been deposited with the Illinois Natural History Survey, Champaign, IL.

Data analysis.

For each experiment, data were analyzed separately for each of the cerambycid species that were caught in greatest numbers (≥ 14 specimens). Differences between treatments in mean numbers of beetles caught, blocked by transect and collection date, were tested with the non-parametric Friedman's test (PROC FREQ with CMH option; SAS Institute 2011) because data violated assumptions of analysis of variance (Sokal and Rohlf 1995). Thus, replicates were defined by trap transect and collection date. Assuming a significant overall test, pairs of treatment means were compared using the Ryan-Einot-Gabriel-Welsch *Q* (REGWQ) multiple comparison test, which controls for maximum experiment-wise error rates (SAS Institute 2011). Replicates containing no beetles of the species in question were dropped from analyses. Differences between treatments in species richness (i.e., the number of cerambycid species represented) were compared using χ^2 goodness of fit test.

Results

During the two experiments, traps captured 885 cerambycid beetles of 36 species in the subfamilies Cerambycinae, Lamiinae, Lepturinae, Parandrinae, and Prioninae, and one species in the closely related family Disteniidae (Table 5.1). Many of the species (N = 18, or ~49%) were represented by five or fewer specimens, with nine species represented by only a single specimen. *Xylotrechus colonus* (F.), of the subfamily Cerambycinae, was caught in greatest numbers in both experiments (457 specimens, or ~52% of the total; Table 5.1), followed by the cerambycine *Neoclytus m. mucronatus* (F.) and three species in the subfamily Lamiinae, *Graphisurus fasciatus* (Degeer), *Astylidius parvus* (LeConte), and *Lepturges angulatus* (LeConte).

In Experiment 1, the trap lure treatments did not differ significantly in the number of species that were represented in trap catch, with cerambycid beetles of 21, 21, 15, and 13 species caught by traps baited with pheromone + fermenting bait, pheromone, fermenting bait, and control lures, respectively ($\chi^2 = 7.1$, $P > 0.05$). Nevertheless, traps baited with the pheromone blend caught significantly more cerambycid beetles in general (i.e., totaled across species) than did control traps (Fig. 5.1A), and trap catch was even greater for the combination of pheromone + fermenting bait (Friedman's $Q_{3,212} = 88.4$, $P < 0.0001$), suggesting that the fermenting bait enhanced attraction. When tested alone, however, the fermenting bait attracted few beetles (Fig. 5.1A).

The significant lure treatment effect in Experiment 1 was due primarily to the cumulative responses of the most numerous species, none of which were significantly attracted by fermenting bait alone (Table 5.2). Adults of *X. colonus* were significantly attracted by the pheromone blend, and attraction was enhanced by the fermenting bait (Table 5.2). On the other hand, adults of *G. fasciatus* were significantly attracted only by the combination of pheromones

and fermenting bait. Adults of *N. m. mucronatus*, *A. parvus*, and *L. angulatus* apparently were equally attracted by the pheromone blend with and without fermenting bait (Table 5.2), indicating that the fermentation volatiles were not affecting attraction. The response to experimental treatments was not strong enough to statistically discriminate between treatments for the cerambycines *Anelaphus pumilus* (Newman), *Sarosesthes fulminans* (F.), and the lamiine *Graphisurus despectus* (LeConte) (Table 5.2).

During Experiment 2, the number of cerambycid species represented in the trap catches again was not significantly influenced by either the lure nor the trap height treatment, with cerambycid beetles of 13, 16, 10, and 6 species being found in traps baited with the pheromone + fermenting bait, pheromone, fermenting bait, and control treatments, respectively ($\chi^2 = 4.9$, $P > 0.05$), and with 16 species each in the understory versus mid-canopy treatments ($\chi^2 = 0$, $P = 1$). Traps baited with pheromones caught more beetles than those having only the fermenting bait, or control traps, but in this case attraction was not significantly influenced by the addition of a fermenting bait (Fig. 5.1B; Friedman's $Q_{3,92} = 45.2$, $P < 0.0001$). Again, the overall pattern of treatment effects was strongly influenced by the most numerous species (Table 5.2). That is, adults of *X. colonus* were significantly attracted by the pheromone blend, and attraction was enhanced by the fermenting bait. Adults of *N. m. mucronatus* and *A. parvus* also were significantly attracted by the pheromone blend, but apparently not influenced by fermenting bait. The response to experimental treatments was not strong enough to statistically discriminate between treatments for the lamiine *G. fasciatus* (LeConte).

During Experiment 2, traps in the forest understory caught significantly greater numbers of beetles than did traps in the canopy (means 6.0 ± 1.2 and 3.7 ± 0.75 beetles, respectively; Friedman's $Q_{1,46} = 5.0$, $P = 0.025$). Among the most numerous species, two were trapped in

greater numbers in the forest understory, including *X. colonus* (3.9 ± 0.6 and 1.3 ± 0.3 beetles per replicate for understory and canopy, respectively; $Q_{1,50}$ = 14.2, P = 0.0002), and *G. fasciatus* (1.5 ± 0.4 and 0.25 ± 0.16 beetles, $Q_{1,16}$ = 4.5, P = 0.034). On the other hand, most adults of *N. m. mucronatus* were caught by traps in the canopy (0.23 ± 0.1 and 1.9 ± 0.5 beetles per replicate, $Q_{1,26}$ = 6.23, P = 0.013). Adults of *A. parvus* were caught in similar numbers by traps at the two heights (1.0 ± 0.29 versus 1.1 ± 0.5 beetles, respectively; $Q_{1,18}$ = 0.01, P > 0.05).

Discussion

The species which were represented by the greatest number of specimens already were known to be attracted by the same blend of synthesized pheromones from previous studies (e.g., Hanks et al. 2012, Hanks and Millar 2013, Handley et al. 2015). Adults of *X. colonus* were attracted by the blend because it contains all four components of the pheromone produced by males of this species, including (*R*)- and (*S*)-3-hydroxyhexan-2-one, and (2*R,*3*R*)- and (2*S,*3*S*)-2,3-hexanediol (Lacey et al. 2009, Hanks et al. 2012). Moreover, (*R*)-3-Hydroxyhexan-2-one also comprises the sole or dominant pheromone component of *A. pumilus, N. m. mucronatus*, and *Sarosesthes fulminances* (Lacey et al. 2007, 2009; Mitchell et al. 2015). Finally, the fuscumol and fuscumol acetate components of the blend are known to be pheromone components of the lamiines *A. parvus* and *L. angulatus* (Meier et al. 2016), and are likely pheromones for *G. fasciatus* (Mitchell et al. 2011).

The only species significantly influenced by volatiles from the fermenting bait were the cerambycine *X. colonus* and the lamiine *G. fasciatus*, with the bait enhancing attraction to the pheromone blend. Adults of both species have been reported to be attracted by fermenting bait (e.g., Galford 1980). This finding suggests that adults of *X. colonus* feed on fermenting tree sap,

as do adults of some other species of cerambycines (Linsley 1959). Nevertheless, the fermenting bait used in the present study attracted insignificant numbers of that species when tested alone. This inconsistency likely is due to differences between studies in the formulation of the fermenting baits. Different combinations of fruit, sources of sugar and yeast, and alcoholic beverages undoubtedly will yield unique volatile profiles as they ferment, which may result in their attracting different species of insects (Galford 1980). Moreover, the volatile profiles of these baits will evolve over time, beginning with anaerobic production of ethanol, followed by acidic fermentation and production primarily of acetic acid, and then putrefaction (Frost and Dietrich 1929, and references therein). Thus, standardizing volatile profiles, both in terms of the initial formulation and its fermentation in the field, poses a challenge to developing these types of baits as reliable trap attractants. Inconsistency in volatile profiles of fermenting baits may explain why the bait used in the earlier study (Schmeelk et al. 2016), which was tested at the same site as used in the present study, attracted significant numbers of the cerambycine *Eburia quadrigeminata* (Say), whereas this species was not attracted in significant numbers during the present study.

The apparent preference in adults of *X. colonus* for traps in the forest understory also is consistent with the findings of Schmeelk et al. (2016). Adults of this species likely prefer this height because males and females aggregate on larval hosts such as downed hardwood trees and fallen branches. Moreover, adults of *X. colonus* do not feed (Gardiner 1960, Waters 1981, L.M.H., unpublished data), although they may take in sugar water when presented, and so do not need to disperse into the forest canopy in search of food. Preference in *N. m. mucronatus* for mid-canopy traps is difficult to interpret because there is no published information on how the beetles are distributed on their host plants.

The findings of this study provide further evidence that the species diversity of cerambycid communities, and population densities of their species, would be most accurately assessed by positioning traps at multiple heights within the forest canopy. The lack of significant attraction to fermenting bait, and the fact that it moderately enhanced attraction to pheromones for only two species, suggests that such baits hold little promise for improving methods of trapping cerambycids. Nevertheless, only one type of fermenting bait was tested during the present study. It is possible that other formulations could be developed, with different odor profiles, which might be more effective in attracting cerambycids than the bait used in the present study.

Acknowledgments

We thank J. A. Mongold-Diers for assistance in preparing trap lures, S. Vachula for assistance with field work, and J. G. Millar for his helpful comments on an early draft of the manuscript. We appreciate funding support from The Alphawood Foundation of Chicago (to Lawrence M. Hanks), and USDA National Institute of Food and Agriculture (grant number 2012-67013-19303; to LMH).

References

Allison, J. D., C. W. Johnson, J. R. Meeker, B. L. Strom, and S. M. Butler. 2011. Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. J. Econ. Entomol. 104: 1258–1264.

Allison, J. D., B. D. Bhandari, J. L. McKenney, and J. G. Millar. 2014. Design factors that influence the performance of flight intercept traps for the capture of longhorned beetles (Coleoptera: Cerambycidae) from the subfamilies Lamiinae and Cerambycinae. PLoS ONE 9: e93203.

Álvarez, G., I. Etxebeste, D. Gallego, G. David, L. Bonifacio, H. Jactel, E. Sousa, and J. A. Pajares. 2014. Optimization of traps for live trapping of pine wood nematode vector *Monochamus galloprovincialis*. J. Appl. Entomol. 139: 618–626.

Bouget, C., H. Brustel, A. Brin, and T. Noblecourt. 2008. Sampling saproxylic beetles with window flight traps: methodological insights. Rev. Écol. (Terre Vie), suppt. 10: 21–32.

Brockerhoff, E. G., A. M. Liebhold, and H. Jactel. 2006. The ecology of forest insect invasions and advances in their management. Can. J. For. Res. 36: 263–268.

Champlain, A. B., and J. N. Knull. 1932. Fermenting bait traps for trapping Elateridae and Cerambycidae (Coleop.). Entomol. News 43: 253–257.

Dodds, K. J., J. D. Allison, D. R. Miller, R. P. Hanavan, and J. Sweeney. 2015. Considering species richness and rarity when selecting optimal survey traps: comparisons of semiochemical baited flight intercept traps for Cerambycidae in eastern North America. Ag. For. Entomol. 17: 36–47.

Frost, S. W., and H. Dietrich. 1929. Coleoptera taken from bait-traps. Ann. Entomol. Soc. Am. 22: 427–436.

Galford, J. R. 1980. Research Note NE-293 Bait bucket trapping for red oak borers (Coleoptera: Cerambycidae). U. S. Dept. Ag. For. Serv., Broomall, PA.

Gardiner, L. M. 1960. Descriptions of immature forms and biology of *Xylotrechus colonus* (Fab.) (Coleoptera: Cerambycidae). Can. Entomol. 92: 820–825.

Graham, E. E., R. F. Mitchell, P. F. Reagel, J. D. Barbour, J. G. Millar, and L. M. Hanks. 2010. Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles. J. Econ. Entomol. 103: 641–647.

Graham, E. E., T. M. Poland, D. G. McCullough, and J. G. Millar. 2012. A comparison of trap type and height for capturing cerambycid beetles (Coleoptera). J. Econ. Entomol. 105: 837–846.

Handley, K., J. Hough-Goldstein, L. M. Hanks, J. G. Millar, and V. D'Amico. 2015. Species richness and phenology of cerambycid beetles in urban forest fragments of northern Delaware. Ann. Entomol. Soc. Am. 108: 251–262.

Hanks, L. M., and J. G. Millar. 2013. Field bioassays of cerambycid pheromones reveal widespread parsimony of pheromone structures, enhancement by host plant volatiles, and antagonism by components from heterospecifics. Chemoecology 23: 21–44.

Hanks, L. M., and Q. Wang. 2016. Reproductive biology of cerambycid beetles. *In* Q. Wang (ed.) Cerambycidae of the world: biology and management. CRC Press/Taylor & Francis, Boca Raton, FL (in press).

Hanks, L. M., J. G. Millar, J. A. Mongold-Diers, J.C.H. Wong, L. R. Meier, P. F. Reagel, and R. F. Mitchell. 2012. Using blends of cerambycid beetle pheromones and host plant volatiles to simultaneously attract a diversity of cerambycid species. Can. J. For. Res. 42: 1050–1059.

Hughes, C. C., R. C. Johns, and J. D. Sweeney. 2014. A technical guide to installing beetle traps in the upper crown of trees. J. Acad. Entomol. Soc. 10: 12–18.

Lacey, E. S., J. A. Moreira, J. G. Millar, A. M. Ray, and L. M. Hanks. 2007. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus mucronatus mucronatus*. Entomol. Exp. Appl. 122: 171–179.

Lacey, E. S., J. G. Millar, J. A. Moreira, and L. M. Hanks. 2009. Male-produced aggregation pheromones of the cerambycid beetles *Xylotrechus colonus* and *Sarosesthes fulminans*. J. Chem. Ecol. 35: 733–740.

Linsley, E. G. 1959. Ecology of Cerambycidae. Annu. Rev. Entomol. 4: 99–138.

Meier, L. R., Y. Zou, J. G. Millar, J. A. Mongold-Diers, and L. M. Hanks. 2016. Synergism between enantiomers creates species-specific pheromone blends and minimizes cross-attraction for two species of cerambycid beetles. J. Chem. Ecol. (submitted).

Millar J. G., and L. M. Hanks. 2016. Chemical ecology of cerambycid beetles. *In* Q. Wang (ed.) Cerambycidae of the world: biology and pest management. CRC Press/Taylor & Francis, Boca Raton, FL (in press).

Miller, D. R., and C. M. Crowe. 2009. Length of multiple-funnel traps affects catches of some bark and wood boring beetles in a slash pine stand in northern Florida. Fla. Entomol. 92: 506–507.

Mitchell R. F., E. E. Graham, J.C.H. Wong, P. F. Reagel, B. L. Striman, G. P. Hughes, M. A. Paschen, M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2011. Fuscumol and fuscumol acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. Entomol. Exp. Appl. 141: 71–77.

Mitchell, R. F., P. F. Reagel, J.C.H. Wong, L. R. Meier, W. Dias Silva, J. Mongold-Diers, J. G. Millar, and L. M. Hanks. 2015. Cerambycid beetle species with similar pheromones are segregated by phenology and minor pheromone components. J. Chem. Ecol. 41: 431-440.

Monné, M. A., and F. T. Hovore. 2005. Checklist of the Cerambycidae (Coleoptera) of the Western Hemisphere. BioQuip, Rancho Dominguez, CA.

Nowak, D. J., J. E. Pasek, R. A. Sequeira, D. E. Crane, and V. C. Mastro. 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. J. Econ. Entomol. 94: 116–122.

Ray, A. M., R. A. Arnold, I. Swift, P. A. Schapker, S. McCann, C. J. Marshall, J. S. McElfresh, and J. G. Millar. 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.

SAS Institute. 2011. SAS/STAT Users Guide release 9.3. SAS Institute, Cary, NC.

Schmeelk, T. C., J. G. Millar, and L. M. Hanks. 2016. Influence of trap height and bait type on abundance and species diversity of cerambycid beetles captured in forests of east-central Illinois. J. Econ. Entomol. (in press).

Silk, P. J., J. Sweeney. J. Wu. J. Price, J. M. Gutowski, and E. G. Kettela. 2007. Evidence for a male–produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). Naturwissenschaften 94: 697–701.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

Sweeney, J. D., P. de Groot, L. MacDonald, S. Smith, C. Cocquempot, M. Kenis, and J. M. Gutowski. 2004. Host volatile attractants and traps for detection of *Tetropium fuscum*

(F.), *Tetropium castaneum* L., and other longhorned beetles (Coleoptera: Cerambycidae). Environ. Entomol. 33: 844–854.

Vance, C. C., K. R. Kirby, J. R. Malcolm, and S. M. Smith. 2003. Community composition of longhorned beetles (Coleoptera: Cerambycidae) in the canopy and understorey of sugar maple and white pine stands in south-central Ontario. Environ. Entomol. 32: 1066–1074.

Waters, D. J. 1981. Life history of *Neoclytus acuminatus* with notes on other cerambycids associated with dead or dying deciduous trees. Master's thesis, Auburn University, Auburn, Alabama.

Wermelinger B., P. F. Flückiger, M. K. Obrist, and P. Duelli. 2007. Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. J. Appl. Entomol. 131: 104–114.

Tables

Table 5.1. Number of cerambycid beetles captured by panel traps in forested study sites of east-central Illinois during Experiments 1 and 2.

Taxonomy	Expt. 1	Expt. 2	Total
Cerambycinae			
Anaglyptini			
Cyrtophorus verrucosus (Olivier)	2		2
Clytini			
Neoclytus a. acuminatus (F.)	13	6	19
Neoclytus m. mucronatus (F.)	63	28	91
Neoclytus scutellaris (Olivier)	8		8
Sarosesthes fulminans (F.)	17		17
Xylotrechus colonus (F.)	354	103	457
Eburiini			
Eburia quadrigeminata (Say)	6	3	9
Elaphidiini			
Anelaphus pumilus (Newman)	19		19
Anelaphus villosus (F.)	12		12
Elaphidion mucronatum (Say)	11	1	12
Parelaphidion aspersum (Haldeman)	4	3	7
Parelaphidion incertum (Newman)		1	1
Neoibidionini			
Heterachthes quadrimaculatus Haldeman	1	4	5
Tillomorphini			
Euderces picipes (F.)	8	2	10
Lamiinae			
Acanthocinini			
Astyleiopus variegatus (Haldeman)	5		5
Astylidius parvus (LeConte)	16	19	35
Astylopsis macula (Say)	6		6
Graphisurus despectus (LeConte)	15	12	27
Graphisurus fasciatus (Degeer)	39	14	53
Hyperplatys maculata Haldeman	3		3
Lepturges angulatus (LeConte)	35		35
Lepturges confluens (Haldeman)	1	2	3
Sternidius alpha (Say)	5	1	6
Sternidius misellus (LeConte)	1		1
Urgleptes foveatocollis (Hamilton)	1		1
Urgleptes querci (Fitch)	1	1	2

Table 5.1 (cont.).

Taxonomy	Expt. 1	Expt. 2	Total
Acanthoderini			
Aegomorphus modestus (Gyllenhal)	9	7	16
Desmiphorini			
Eupogonius pauper LeConte	1		1
Psenocerus supernotatus (Say)	1		1
Dorcaschematini			
Dorcaschema cinereum (Olivier)		1	1
Saperdini			
Saperda lateralis F.	1		1
Lepturinae			
Lepturini			
Brachyleptura rubrica (Say)	1		1
Typocerus lugubris (Say)	4		4
Rhagiini			
Gaurotes cyanipennis (Say)	1		1
Parandrinae			
Parandrini			
Neandra brunnea (F.)	2		2
Prioninae			
Prionini			
Orthosoma brunneum (Forster)	4	2	6
Disteniidae			
Elytrimitatrix undata (F.)	4	1	5
Total	**661**	**224**	**885**

Table 5.2. Mean (± 1 SE) number of beetles caught per replicate by experimental treatment for the cerambycid species represented by the greatest numbers of specimens (N ≥ 14) in Experiments 1 and 2, and results of Friedman's tests. Asterisks indicate significance level of Friedman's *Q*: * $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$. Means with different letters within species are significantly different (REGWQ test, $P < 0.05$). Overall analyses for *A. pumilus* and *S. fulminans* in Experiment 1 were significant at $P < 0.01$, but the means separation test failed to detect differences between pairs of means.

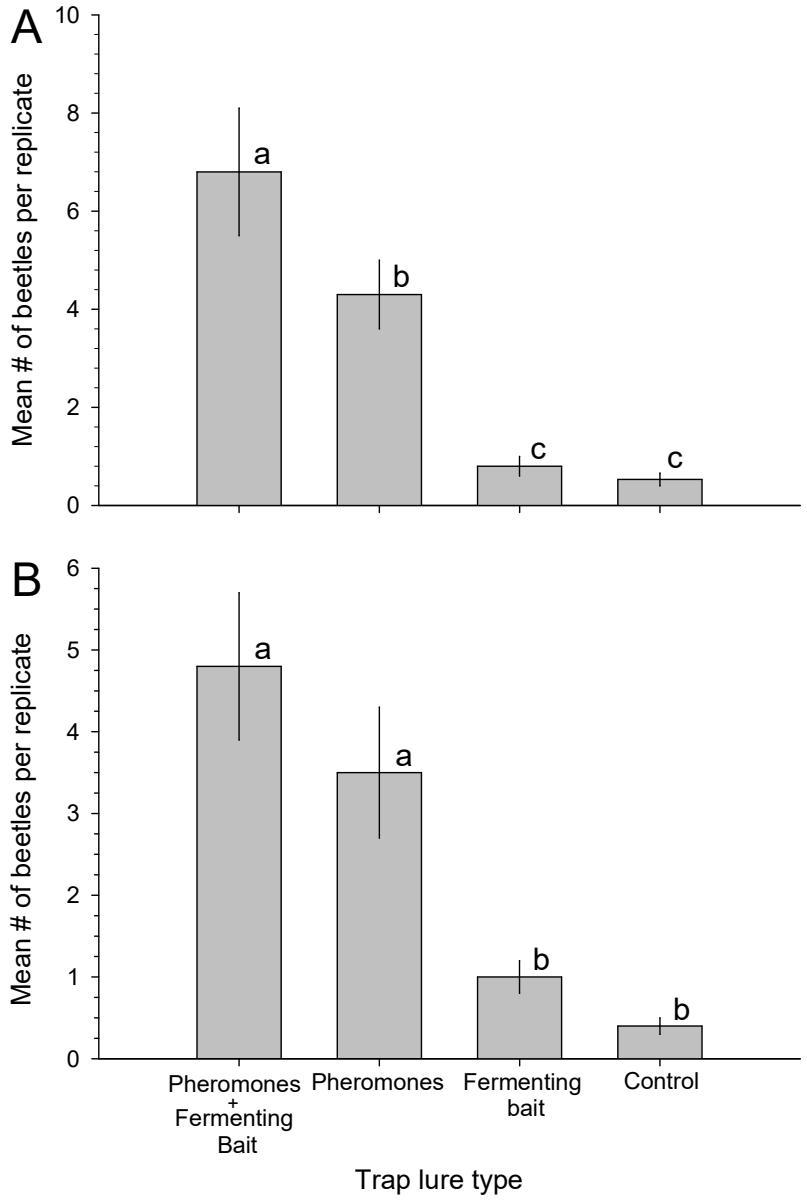
Species	Pheromones + Fermenting bait	Pheromones	Fermenting bait	Control	Friedman's *Q* (df)
Experiment 1					
Cerambycinae					
Anelaphus pumilus	2.5 ± 1.3	2.3 ± 1.3	0	0	8.36 (16)*
Neoclytus m. mucronatus	1.3 ± 0.3a	1.0 ± 0.2a	0.08 ± 0.05 b	0b	38.3 (104)***
Sarosesthes fulminans	1.0 ± 0.41	0.78 ± 0.04	0.11 ± 0.01	0	9.8 (36)*
Xylotrechus colonus	4.6 ± 0.7a	2.6 ± 0.4b	0.49 ± 0.1c	0.16 ± 0.08c	86.6 (180)***
Lamiinae					
Astylidius parvus	0.46 ± 0.2ab	0.69 ± 0.1a	0.08 ± 0.08bc	0b	15.4 (52)**
Graphisurus despectus	0.77 ± 0.3	0.33 ± 0.2	0.22 ± 0.2	0.33 ± 0.2	3.65 (36)
Graphisurus fasciatus	1.4 ± 0.37a	0.61 ± 0.2b	0.11 ± 0.1b	0.06 ± 0.06b	20.0 (72)**
Lepturges angulatus	0.92 ± 0.3a	0.92 ± 0.2a	0b	0b	22.0 (52)***
Experiment 2					
Cerambycinae					
Neoclytus m. mucronatus	1.2 ± 0.38a	0.69 ± 0.2ab	0.23 ± 0.2b	0b	13.9 (52)**
Xylotrechus colonus	3.35 ± 0.5a	1.5 ± 0.4b	0.2 ± 0.09c	0.15 ± 0.08c	40.4 (80)***

Table 5.2 (cont.).

Species	Pheromones + Fermenting bait	Pheromones	Fermenting bait	Control	Friedman's *Q* (df)
Lamiinae					
Astylidius parvus	1.0 ± 0.5a	1.11 ± 0.2a	0b	0b	17.9 (36)**
Graphisurus fasciatus	0.63 ± 0.26	0.5 ± 0.27	0.38 ± 0.26	0.25 ± 0.16	0.44 (32)

Figures

Fig. 5.1. Mean (± 1 SE) number of cerambycid beetles caught per replicate during Experiment 1 (A) and Experiment 2 (B). Means with different letters within experiments are significantly different (REGWQ test, $P < 0.05$).



CHAPTER 6: MORPHOLOGICAL EVIDENCE OF PHEROMONE PRODUCTION IN CERAMBYCID SPECIES NATIVE TO CHINA

Abstract

Increased trade between the United States and China has resulted in exotic pest species establishing in both countries, causing considerable ecological and economic damage. There is global realization of the damage to ecosystems created by invasive species, and while regulatory policies are in place, coordination and implementation is still lacking. Because of ever-increasing trade volume and the similarities in climatic and habitat types between the two countries, a number of important exotic pest species established in the United States have come from China (e.g., the Asian longhorned beetle, *Anoplophora glabripennis* [Motschulsky] and Velvet longhorned beetle, *Trichoferus campestris* [Faldermann]).

Many species of cerambycid beetles in the large subfamily Cerambycinae have been shown to use aggregation-sex pheromones, produced by males, which share a structural motif: unbranched hydrocarbons that are six, eight, or ten carbons long with hydroxyl or carbonyl groups on carbons two and three. These pheromones are emitted from glands in the prothorax of males that connect by ducts to pores on the cuticular surface. The glands, and the pores, are absent in females. Here, we describe a morphological survey, by scanning electron microscopy, of cerambycine species native to China which was intended to assess the probability that the species use pheromones of the diol-ketol motif. Gland pores were found to be present in males and absent in females in all 22 of the species that were examined. Species varied in the general morphology of the gland pores and how they were distributed on the prothorax.

Introduction

Increase in trade between the United States and China, two countries which share similar ecosystem types, has resulted in establishment of exotic pest species which have caused considerable ecological and economic damage (Normile 2004). United States and China are both leading contributors to, and victims of, the spread of invasive species worldwide. Prevention of introductions, control, and eradication of these exotic species should be of top priority. There is global realization of the problems brought on by invasive species, and international coordination in management tools and regulatory policies are instrumental in minimizing potential damage and risks of invasions, although both coordination and implementation is still lacking. Because of increased trade volume and the similarities in ecosystems, a number of important exotic pest species established in the United States come from China (i.e., Asian longhorned beetle, *Anoplophora glabripennis* [Motschulsky] and Velvet longhorned beetle, *Trichoferus campestris* [Faldermann]).

The wood-boring larvae of cerambycid beetles are among the most important insect pests of woody plants worldwide, because they can damage and kill their host plants, and degrade wood destined for the lumber industry (e.g., Solomon 1995). Because the larvae are endophytic, sequestered within the wood tissues, they are difficult to detect and readily transported by international commerce, and several species have become devastating pests as exotic and invasive species (Haack 2006).

During the past decade, pheromones have been identified for more than 100 species of cerambycids, and this research has revealed a remarkable degree of parsimony in chemical structures of pheromones among closely related species (i.e., congeners), and even among species in different subfamilies (reviewed by Millar and Hanks 2016). All species in the

subfamily Cerambycinae studied to date use volatile aggregation-sex pheromones (sensu Cardé 2014) which are produced by males and attract both sexes. A very common pheromone motif among cerambycines is unbranched chains of six, eight, or ten carbons with hydroxyl or carbonyl groups on carbons two and three (i.e., diols and ketols; Millar and Hanks 2016). The glands which produced these pheromones has been identified for several cerambycine species to date, and invariably are in the prothorax of males, connecting via ducts to pores on the cuticular surface (e.g., Iwabuchi 1986, Noldt et al. 1995, Hoshino et al. 2015). The glands and the pores are absent in females.

The male-specificity of the pheromone gland pores suggested to Ray et al. (2006) that they could be used to assess the probability that a given cerambycine species uses an aggregation-sex pheromone of the diol-ketol motif. Those authors examined the prothoraces from both sexes of 65 species of cerambycines, most of which were native to the Americas, and discovered that 49 species had male-specific pores, while the pores were absent in both sexes of the remaining 16 species. The position of the pores on the prothorax of males, and their ultrastructure, was quite variable across species (Ray et al. 2006). Similar findings were reported by Li et al. (2013) for nine species of cerambycines from Jilin, China, and by Hoshino et al. (2015) for 26 species of cerambycines from Japan.

The hypothesis that the prothoracic pores of males can be used to predict pheromone chemistry has since been supported for several of the study species of Ray et al. (2006), the males later found to produce pheromones of the diol-ketol motif (Lacey et al. 2007a,b; Hanks et al. 2007; Ray et al. 2009b; Zou et al. 2016). Also supporting the hypothesis is the cerambycine *Rosalia funebris* Motschulsky, which lacks the gland pores, because males produce a pheromone

of very different structure ([*Z*]-3-decenyl [*E*]-2-hexenoate) from as yet unidentified glands (Ray et al. 2009a).

Here, we describe a morphological survey, by scanning electron microscopy, of cerambycine species native to China which was intended to assess the probability that those Asian species use pheromones of the diol-ketol motif. Adult males and females of 22 cerambycine species were collected in the Yunnan Province of China during field bioassays of synthesized pheromones (see below, Wickham et al. 2014), and their prothoraces were imaged by scanning electron microscopy to determine whether males had pores that were absent in females, and to characterize their ultrastructure. This research contributes to knowledge on the chemical ecology of cerambycids from China.

Methods

Sources of chemicals.

All compounds used in the 2010 experiment (see below) were synthesized at the University of California, Riverside, including *syn*-2,3-hexanediol, *anti*-2,3-hexanediol, *syn*-2,3-octanediol, *anti*-2,3-octanediol (following the methods of Lacey et al. 2004), 3-hydroxyoctan-2-one, 3-hydroxyhexan-2-one, and 3-hydroxydecan-2-one (Lacey et al. 2007a), 2-(undecyloxy)ethanol (termed monochamol; Pajares et al. 2010), (*Z/E*)-6,10-dimethyl-5,9-undecadien-2-ol (fuscumol), and (*Z/E*)-6,10-dimethyl-5,9-undecadien-2-ol acetate (fuscumol acetate; Mitchell et al. 2011). In 2013, 3-hydroxyhexan-2-one and monochamol were purchased from Bedoukian Research (Danbury, CT).

Sources of beetle specimens.

Beetles were captured during two field experiments conducted in the Yunnan Province China in 2010 and 2015 (Wickham et al. 2014). Lures included pheromones that are typical of cerambycines (and of the diol-ketol motif), including *syn*-2,3-hexanediol, *anti*-2,3-hexanediol, *syn*-2,3-octanediol, *anti*-2,3-octanediol, 3-hydroxyhexan-2-one, 3-hydroxyoctan-2-one, and 3-hydroxydecan-2-one, as well as pheromones of very different structure which are typical of species in the subfamily Lamiine, including monochamol, (*Z/E*)-fuscumol, and (*Z/E*)-fuscumol acetate (see Millar and Hanks 2016). Although it might seem that garnering specimens from field experiments using pheromones would bias the findings in favor of species that produce pheromones, only eight of the 21 species of cerambycines that were caught during the study showed significant attraction to the synthesized pheromones. The remaining species were caught in small numbers, perhaps passively by traps (e.g., see Hanks et al. 2014). Results from one experiment were reported by Wickham et al. (2014) and the results from the second field experiment will be published in the future. Cerambycid beetles that were caught during the two field experiments were identified using the keys in Gressitt (1951), Gressitt et al. (1970), and Hua et al. (2009). Voucher specimens have been deposited in the museum collection of Guangxi University, Guangxi, China.

Scanning electron microscopy.

Single specimens of males and females of each species were imaged by scanning electron microscopy to determine whether the male-specific pores were present, and if so, to characterize their morphology and distribution on the prothorax. Previous work had confirmed that, whereas the number and general morphology of the pores may vary among conspecifics, within a species

they do not vary as to whether they have the male-specific pores or not (e.g., Ray et al. 2006; unpub. data). The specimens were cleaned of debris and lipids by first soaking them overnight in 4% Triton X100 solution (Sigma Aldrich, St. Louis, MO, USA). They then were dehydrated by submerging them, sequentially, in 70, 95 and 99% ethanol for 5 min each. Finally, they were soaked in mixed hexanes (Fisher Scientific, Fairlawn, NJ, USA) for at least 2 h, sonicated in the hexanes for 30 sec, and allowed to air-dry overnight. We attached multiple specimens to aluminum mounts with double-sided adhesive carbon discs. Samples were sputter coated with 7 μm of gold-palladium (Desk II TSC turbo sputter coater, Denton Vacuum, Moorestown, NJ, USA). Mounts were stored in a desiccator. The specimens were imaged specimens with a Quanta FEG 250 environmental scanning electron microscope (FEI Company, Hillsboro, OR, USA) at 5.0 kV. We imaged the pronotum and the prosternum of each specimen.

Results

During the 2010 and 2013 field experiments, adult beetles of both sexes were collected for 22 species of cerambycines (Table 6.1), including representatives of four tribes, with most of the species in the tribe Clytini. Scanning electron microscopy revealed that males of all 22 species had conspicuous pores on their prothoraces that were absent in conspecific females (Table 6.1). An example is *Xylotrechus lateralis fracturis* Guo & Chen (Fig. 6.1), males of which had indentations scattered across the sides of the pronotum within which were groups of pores. Males of most of the species had the pores grouped within such indentations, the indentations being roughly circular to elongate and ~5 - 50 μm along their greatest axis (Figs. 6.1e, 6.2, 6.3). The number of pores within indentations was highly variable even within individuals, and also between species. Only four species had single pores (i.e., not in groups): *Demonax occulatus*

Gressitt & Rondon (Fig. 6.2c), *Demonax theresae* Pic (Fig. 6.2e), and *Perissus griseus* Gressitt (Fig. 6.3b), and *Artimpaza lineata* (Pic) (not shown). The morphology of the male-specific pores varied considerably even among congeners, such as among congeners of *Demonax* and *Rhaphuma* (Fig. 6.2), and among congeners of *Perissus* and *Xylotrechus* (Fig. 6.3).

Discussion

The presence of the male-specific gland pores in all of the species in the present study is consistent with the growing evidence that mate location in cerambycid beetles is mediated by male-produced aggregation-sex pheromones for species in the subfamilies Cerambycinae, Lamiinae, and Spondylidinae, and by female-produced sex pheromones for species in the Lepturinae and Prioninae (Millar and Hanks 2016). Nevertheless, males of at least some species of cerambycines, such as *R. funebris*, produce pheromones of different structure from unknown glands, and lack the male-specific pores on the prothorax (Ray et al. 2009a). Our sampling of species is biased, however, because most of our study species were in the tribe Clytini, as also was true for the study species of Li et al. (2013) and Hoshino et al. (2015). Nearly all the clytine species studied to date have the male-specific pores (e.g., Ray et al. 2006, Hanks et al. 2007; also see below). In the present study, variation in the structure of prothoracic gland pores within individuals, and between study species, and in how the pores are distributed on the prothorax, is consistent with these earlier morphological studies of cerambycids.

The function of the male-specific prothoracic pores has been confirmed formally for only a few cerambycine species to date (Iwabuchi 1986, Noldt et al. 1995, Hoshino et al. 2015), but the pores have been associated with pheromone production for many more species (see Millar and Hanks 2016). Among the species considered here, field bioassays from which the specimens

were drawn have demonstrated attraction to synthesize pheromones of the diol-ketol motif for several species, including attraction to 3-hydroxyhexan-2-one in *D. graciles striatus*, *X. a. draconiceps*, and *X. incurvatus*, attraction to *anti*-2,3-hexanediol in *Rhaphuma laosica* Gressitt & Rondon, and attraction to *anti*-2,3-octanediol in *D. theresae* (Wickham et al. 2014). Males of *X. chinensis* already were known to produce a pheromone comprised of eight carbon diols and ketols (Iwabuchi et al. 1987), and the structure of the gland pores as described by Hoshino et al. (2015) was similar to that reported here.

Field bioassays of pheromones, such as those which were the source of our specimens, create inherently one-sided tests. That is, attraction of a species to a particular compounds is reliable evidence that the compounds is at least a component of the pheromone (Millar and Hanks 2016), but non-responding species do not necessarily lack pheromones. For example, traps baited with a synthesized pheromone blend of a particular species may fail to attract significant numbers of beetles due to methodological problems, such as trapping at the wrong time of year, or positioning traps only at ground level (Millar and Hanks 2016). Of course, adults of a given species are unlikely to be attracted if the trap treatments do not include pheromone components of that species. Moreover, cerambycine species that have pheromones of two or more components may not respond to individual components (e.g., Mitchell et al. 2013, 2015), and such species would not have been attracted by the individual racemic compounds that were tested by Wickham et al. (2014).

Ray et al. (2006) found considerable variation among cerambycine species as to whether they had the male-specific pores or not, but that study cast a broad taxonomic net, including 65 species of 24 tribes of the Cerambycinae. Most of the species that reportedly lacked the pores were the sole representatives of their tribes, so it therefore remains to be seen if this trait is

characteristic of their tribes. On the other hand, data for the tribes that were better represented suggests that there is some variation in the gland pore trait among species that presumably are closely-related (i.e., in the same tribe). For example, the pores were present in all four species of the tribe Callidiini, and all six species of the Trachyderini, but were absent in one of eight species in the Elaphidiini, and one of 21 species of the Clytini. The trait was variable even within the genus *Lissonotus*, one species having the pores, and the other lacking them (Ray et al. 2006). Similarly, Hoshino et al. (2015) reported that the pores were absent in both sexes of the clytine *Xylotrechus cuneipennis* (Kraatz), even though they are known to be present in males of several congeners (Iwabuchi 1986, Ray et al. 2006, Hanks et al. 2007, Lacey et al. 2007, present article).

In conclusion, this study provides further evidence that the diol-ketol pheromone motif is common among cerambycines of Asia, particular those in the tribe Clytini. It also contributes to the growing consensus that mate location is mediated by volatile pheromones for most species of the Cerambycidae. The considerable parsimony in pheromone structures within the family, and across continents, this worldwide phenomenon may be exploited in developing blends of compounds that serve as lures likely to attract a diversity of species, to be used for quarantine surveillance for exotic and potentially invasive species. This is particularly important as many of the current invasive species that have large economic impacts in North America are from China or nearby countries in Asia.

Acknowledgments

We thank S. J. Robinson and C. Wallace for assisting with the SEM work. This research was made possible in part through collaboration with Bugscope, The Imaging Technology Group, Beckman Institute for Advanced Science and Technology, University of Illinois at

Urbana-Champaign (http://bugscope.beckman.uiuc.edu/). We appreciate funding support from the Alphawood Foundation of Chicago (to Lawrence M. Hanks) and USDA-APHIS (grant #15-8130-1422-CA to Jocelyn G. Millar and LMH).

References

Cardé, R. T. 2014. Defining attraction and aggregation pheromones: teleological versus functional perspectives. J. Chem. Ecol. 40: 519–520.

Graham, E. E., R. F. Mitchell, P. F. Reagel, J. D. Barbour, J. G. Millar, and L. M. Hanks. 2010. Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles. J. Econ. Entomol. 103: 641–647.

Gressitt, J. L. 1951. Longicorn beetles of China. Longicornia 2: 1–667.

Gressitt, J. L., J. A. Rondon, and S. von Bruening. 1970. Cerambycid beetles of Laos. Pac. Insects Monogr. 24: 1–651.

Haack, R. A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. 36: 269–288.

Hanks, L. M., J. G. Millar, J. A. Moreira, J. D. Barbour, E. S. Lacey, J. S. McElfresh, and A. M. Ray. 2007. Using generic pheromone lures to expedite identification of pheromones for the cerambycid beetles *Xylotrechus nauticus*, *Phymatodes lecontei*, and *Neoclytus modestus modestus*. J. Chem. Ecol. 33: 889–907.

Hanks, L. M., P. F. Reagel, R. F. Mitchell, J.C.H. Wong, L. R. Meier, C. A. Silliman, E. E. Graham, B. L. Striman, K. P. Robinson, J. A. Mongold-Diers, and J. G. Millar. 2014. Seasonal phenology of the cerambycid beetles of east-central Illinois. Ann. Entomol. Soc. Am. 107: 211–226.

Hoshino, K., S. Nakaba, H. Inoue, and K. Iwabuchi. 2015. Structure and development of male pheromone gland of longicorn beetles and its phylogenetic relationships within the tribe Clytini. J. Exp. Zool. 324B: 68–76.

Hua, L. Z., N. Hajime, G. A. Samuelson, and S. W. Lingafelter. 2009. Iconography of Chinese longicorn beetles. Sun Yat-Sen University Press, Guangzhou, China.

Iwabuchi, K. 1986. Mating behavior of *Xylotrechus pyrrhoderus* Bates (Coleoptera: Cerambycidae) III. Pheromone secretion by male. Appl. Entomol. Zool. 21: 606–612.

Iwabuchi, K., J. Takahashi, and T. Sakai. 1987. Occurrence of 2,3-octanediol and 2-hydroxy-3-octanone, possible male sex pheromone in *Xylotrechus chinensis* Chevrolat (Coleoptera: Cerambycidae). Appl. Entomol. Zool. 22: 110–111.

Lacey, E. S., M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2004. Male-produced aggregation pheromone of the cerambycid beetle *Neoclytus acuminatus acuminatus*. J. Chem. Ecol. 30: 1493–1507.

Lacey E. S., J. A. Moreira, J. G. Millar, A. M. Ray, and L. M. Hanks. 2007a. Male-produced aggregation pheromone of the cerambycid beetles *Neoclytus mucronatus mucronatus*. Entomol. Exp. Appl. 122: 171–179.

Lacey, E. S., A. M. Ray, and L. M. Hanks. 2007b. Calling behavior of the cerambycid beetle *Neoclytus acuminatus acuminatus* (F.). J. Insect Behav. 20: 117–128.

Li, Y., Q. Meng, J. Sweeney, and W. Gao. 2013. Ultrastructure of prothoracic pore structures of longhorn beetles (Coleoptera: Cerambycidae: Cerambycinae) native to Jalin, China. Ann. Entomol. Soc. Am. 106: 637–642.

Millar, J. G., and L. M. Hanks. 2016. Chemical ecology of cerambycid beetles. *In* Q. Wang (ed.) Cerambycidae of the world: biology and pest management. CRC Press/Taylor & Francis, Boca Raton, FL. (in press).

Mitchell, R. F., E. E. Graham, J.C.H. Wong, P. F. Reagel, B. L. Striman, G. P. Hughes, M. A. Paschen, M. D. Ginzel, J. G. Millar, and L. M. Hanks. 2011. Fuscumol and fuscumol

acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. Entomol. Exp. Appl. 141: 71–77.

Mitchell, R. F., J. G. Millar, and L. M. Hanks. 2013. Blends of (*R*)-3-hydroxyhexan-2-one and alkan-2-ones identified as potential pheromones produced by three species of cerambycid beetles. Chemoecology 23: 121–127.

Mitchell, R. F., P. F. Reagel, J.C.H. Wong, L. R. Meier, W. Dias Silva, J. Mongold-Diers, J. G. Millar, and L. M. Hanks. 2015. Cerambycid beetle species with similar pheromones are segregated by phenology and minor pheromone components. J. Chem. Ecol. 41:431-440.

Noldt, U., R. Fettköther, and K. Dettner. 1995. Structure of the sex pheromone-producing prothoracic glands of the male old house borer, *Hylotrupes bajulus* (L.) (Coleoptera: Cerambycidae). Intl. J. Insect Morphol. Embryol. 24: 223–234.

Normile, D. 2004. Expanding trade with China creates ecological backlash. Science 306: 968–969.

Pajares, J. A., G. Álvarez, F. Ibeas, D. Gallego, D. R. Hall, and D. I. Farman. 2010. Identification and field activity of a male-produced aggregation pheromone in the pine sawyer beetle, *Monochamus galloprovincialis*. J. Chem. Ecol. 36: 570–583.

Ray, A. M., E. S. Lacey, and L. M. Hanks. 2006. Predicted taxonomic patterns in pheromone production by longhorned beetles. Naturwissenschaften 93: 543–550.

Ray, A. M., J. G. Millar, J. S. McElfresh, I. P. Swift, J. D. Barbour, and L. M. Hanks. 2009a. Male-produced aggregation pheromone of the cerambycid beetle *Rosalia funebris*. J. Chem. Ecol. 35: 96–103.

Ray, A. M., I. P. Swift, J. A. Moreira, J. G. Millar, and L. M. Hanks. 2009b. (*R*)-3-hydroxyhexan-2-one is a major pheromone component of *Anelaphus inflaticollis* (Coleoptera: Cerambycidae). Environ. Entomol. 38: 1462–1466.

Solomon, J. D. 1995. Agriculture Handbook 706: guide to insect borers of North American broadleaf trees and shrubs. USDA Forest Service, Washington, DC.

Wickham, J. D., R. D. Harrison, W. Lu, Z. Guo, J. G. Millar, L. M. Hanks, and Y. Chen. 2014. Generic lures attract cerambycid beetles in a tropical montane rain forest in southern China. J. Econ. Entomol. 107: 259–267.

Zou, Y., C. F. Rutledge, K. Nakamuta, C. T. Maier, L. M. Hanks, A. B. Richards, E. S. Lacey, and J. G. Millar. 2016. Identification of a pheromone component and a critical synergist for the invasive beetle *Callidiellum rufipenne* (Coleoptera: Cerambycidae). Environ. Entomol. 45: 216–222.

Tables

Table 6.1. Position and structure of prothoracic pores that are presumed to be associated with pheromone glands in males of cerambycid species native to Asia. Pores may occur singly, or multiple pores may be in groups (see Fig. 6.1).

Taxonomy	**Location of pores in males (single versus multiple)**
Tribe Callidiopini	
Ceresium sinicum White	Sides of pronotum (multiple)
Tribe Cleomenini	
Artimpaza lineata (Pic)	Sides of pronotum (single)
Tribe Clytini	
Chlorophorus arciferus (Chevrolat)	Sides of pronotum (multiple)
Chlorophorus reductus Pic	Center and sides of pronotum (multiple)
Demonax graciles striatus Gressitt & Rondon	Sides of pronotum (multiple)
Demonax literatus literatus Gahan	Center and sides of pronotum (multiple)
Demonax occulatus Gressitt & Rondon	Center of pronotum (single)
Demonax pseudonotabilis Gressitt & Rondon	Center and sides of pronotum (multiple)
Demonax theresae Pic	Center and sides of pronotum (single)
Perissus atronotatus Pic	Sides of pronotum (multiple)
Perissus griseus Gressitt	Center and sides of pronotum (single)
Perissus mimicus Gressitt & Rondon	Center and sides of pronotum
Perissus mutabilis obscuricolor Pic	Center and sides of pronotum (multiple)
Rhaphuma anongi Gressitt & Rondon	Center of pronotum (multiple)
Rhaphuma horsfieldi (White)	Sides of pronotum (multiple)
Rhaphuma laosica Gressitt & Rondon	Sides of pronotum (multiple)
Xylotrechus atronotatus draconiceps Gressitt	Posterior edge of sides of pronotum (multiple)
Xylotrechus buqueti (Castelnau & Gory)	Center of pronotum (multiple)
Xylotrechus chinensis (Chevrolat)	Center and sides of pronotum (multiple)

Table 6.1 (cont.).

Taxonomy	**Location of pores in males (single versus multiple)**
Xylotrechus incurvatus (Chevrolat)	Sides of pronotum (multiple)
Xylotrechus lateralis fracturis Guo & Chen	Sides of pronotum (multiple)
Tribe Phoracanthini	
Allotraeus asiaticus (Schwarzer)	Sides of pronotum (multiple)

Figures

Fig. 6.1. Sexual dimorphism in prothorax of the cerambycine beetle *Xylotrechus lateralis fracturis*: a) female; b) male (the rectangular shapes in a and b show roughly the location of c and d); c) close-up of female; d) close-up of male showing indentations that contain pores; e) close up of gland pores lying within indentations on the prothorax of the male.

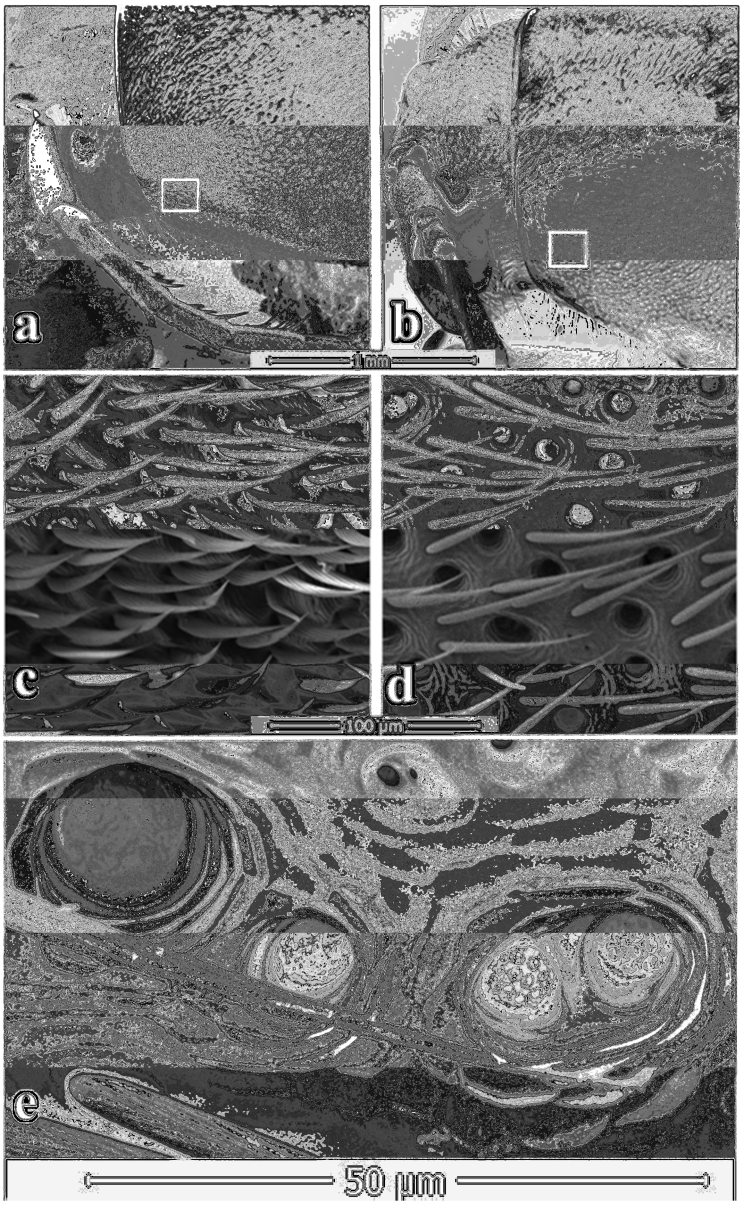


Fig 6.2. Prothoracic pores in males of species in the genus *Demonax*: a) *D. graciles striatus*; b) *D. literatus literatus*; c) *D. occulatus*; d) *D. pseudonotabilis*; e) *D. theresae*; and males of species in the genus *Rhaphuma*: f) *R. anongi*; g) *R. horsfieldi*; h) *R. laosica*.

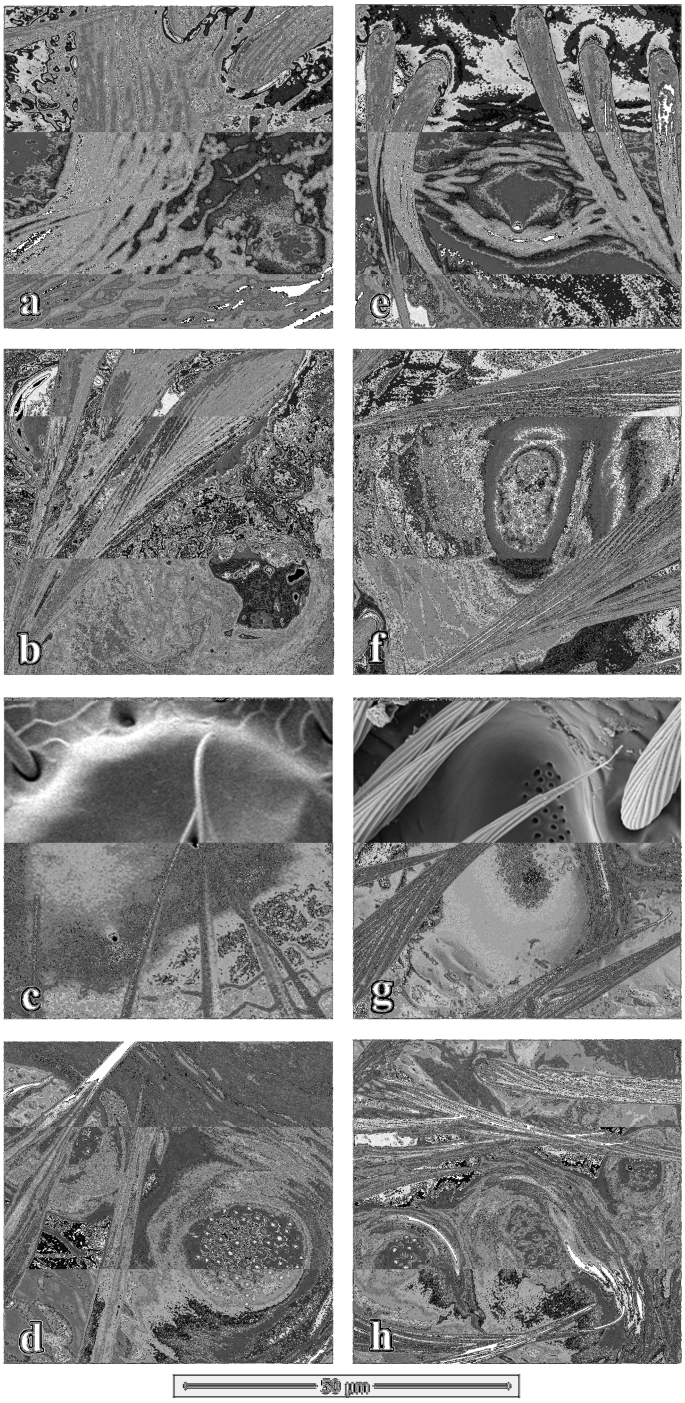
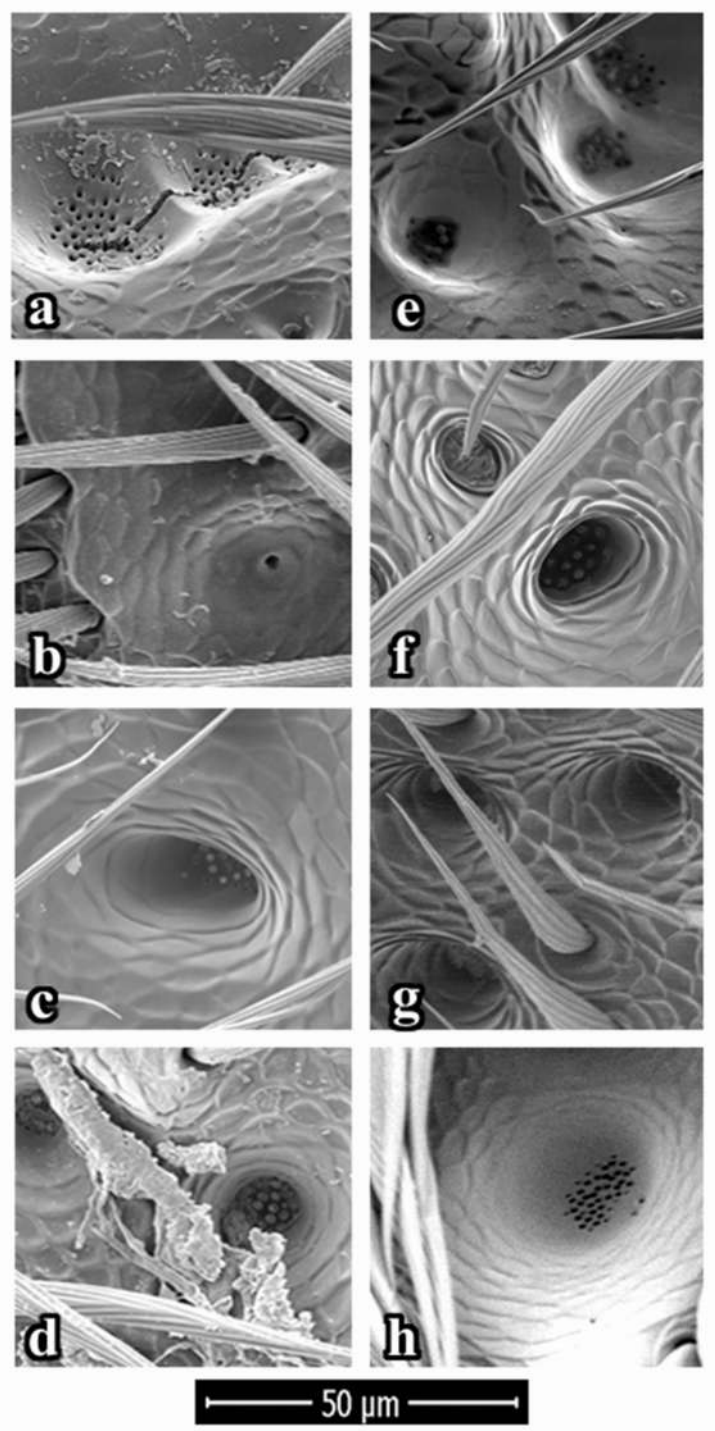



Fig. 6.3. Prothoracic pores in males of species in the genus *Perissus*: a) *P. atronotatus*; b) *P. griseus*; c) *P. mimicus*; d) *P. mutabilis obscuricolor*; and males of species in the genus *Xylotrechus*: e) *X. atronotatus draconiceps*; f) *X. buqueti*; g) *X. chinensis*; h) *X. incurvatus*.