

INFLUENCE OF THE LARVAL HOST PLANT ON REPRODUCTIVE STRATEGIES OF CERAMBYCID BEETLES

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ABSTRACT

This investigation into the natural history and behavior of 81 species of cerambycid beetles suggests that reproductive behavior is correlated with the condition of the larval host: Adults of species whose larvae attack living trees tend to show behavioral differences from those that attack dying or dead hosts. Behavioral differences among species that are associated with larval host condition include: (a) choice of adult food source and whether adults feed at all; (b) mechanisms of mate location and the role of long-range pheromones; (c) vagility and dispersal behaviors of adults; (d) location of the mating site; and (e) duration of copulation.

INTRODUCTION

Long-horned, or longicorn, beetles are so named for their elongate antennae, which may exceed three times the body length in adult males. These are among the most diverse insects, with more than 35,000 species in about 4,000 genera (92) and many more species probably yet undiscovered (e.g. see 148). Cerambycids are phytophagous: the larvae, round-headed borers, usually burrow in the tissues of woody plants in conditions ranging from alive to moribund to dead and decomposing, but some species feed within the stems of living herbaceous plants (e.g. 37, 96). Adaptation to such highly variable host plants has resulted in tremendous variation in the behavior and ecology of these borers,

and many species are important pests of forest, plantation, and street trees (e.g. 37, 96).

The economic importance of cerambycids has inspired study of their taxonomy and larval host relations (e.g. 30, 37–41). Because the adult beetles are large and often attractively colored, they are prized by beetle enthusiasts around the world who have generated a voluminous literature on adult taxonomy and species' geographical distributions. Despite this wealth of general biological information, the behavior of adult cerambycids has received relatively little attention (37, 100), primarily because they cause negligible direct damage and many species are nocturnal and rarely observed. What is known of adult cerambycids suggests that species vary greatly in natural history and reproductive behavior (37, 96). In this article, I address the hypothesis that behaviors and reproductive strategies of adult cerambycids are shaped by host requirements of the larval stage.

SUBFAMILIES OF THE CERAMBYCIDAE

The family Cerambycidae includes at least nine subfamilies that are delineated by morphological characters of adults and larvae (103). Among the larger subfamilies, the most primitive (and in a separate subfamily group from the others) is the Prioninae. More advanced are the Lepturinae and Aseminae, and most advanced are the Cerambycinae and Lamiinae (97, 103). Prionine adults are characterized by relatively large body size and short antennae (for cerambycids) that are often sexually dimorphic in structure (male antennae more branched than those of females; 97). Prionine larvae are usually polyphagous root or trunk feeders associated with decaying hosts (18). The small and anomalous subfamily Anoploderminae may be related to the prionines (103). Lepturine adults are abundant and familiar to collectors because they are diurnal, often brightly colored, and commonly encountered on flowers (37, 97, 100); their short antennae show slight sexual dimorphism in length only (male antennae longer). Because lepturine larvae usually feed on decaying wood (18), they are usually not of economic importance and are rarely studied. Larvae of the Aseminae also feed on dead woody plants and adults have short antennae that are not sexually dimorphic (18, 97).

The Cerambycinae comprise a large, monophyletic group (97, 103) that encompasses a variety of adult morphological types and a diversity of host associations (woody plants that are living, dying, dead, and even seasoned wood). Adults of most cerambycine species have elongate antennae (generally longer than the body) that are conspicuously sexually dimorphic in length (male antennae longer; 97, 103). The Lamiinae, a monophyletic sister group of the Cerambycinae (103) and the largest subfamily (18), also shows a diversity of

host associations (mostly woody angiosperms, a few herbaceous hosts, but rarely dead hosts; see 97). Lamiine adults are distinctive in being hypognathous with a vertical frons (103), characteristics that allow them to gnaw deeply into bark (149). The Cerambycinae and Lamiinae include many species that are among the world's most important pests (18).

LARVAL HOST CONDITION AND REPRODUCTIVE BIOLOGY OF CERAMBYCIDS

Summarizing the Data

The data presented here were gathered mostly from the primary literature to compare the natural history and behavioral characteristics of 81 well-studied species of cerambycids of temperate and tropical regions world wide (Table 1; 1 anoplodermine, 5 asemines, 21 cerambycines, 43 lamiines, 3 lepturines, and 8 prionines). To summarize these data, I calculated means where ranges of values were provided, and also averaged independently published measures of the same parameter for a given species. Because complete information was available for only a few species, comparisons of particular aspects of biology and behavior involved different subsets of the study species. Means were compared by analysis of variance (ANOVA); when transformation failed to render data suitable for ANOVA, the nonparametric Kruskal-Wallis test was used (126). I present untransformed means ± 1 SE throughout.

Categorizing Species by Condition of the Larval Host

Identifying the initial condition of the larval host (i.e. the condition required for colonization by the larva) for wood borers is problematical because researchers rarely have the opportunity to assess condition of a plant prior to discovering that it has come under attack. For that reason, many of the study species were initially considered fully capable of attacking host trees in any state of health, from thriving to decaying, but were later found to restrict their attacks to hosts of a particular condition. Larval host condition may be most difficult to assess for root-feeding species whose larvae feed undetected long before any sign of attack is shown by the host plant. *Prionus californicus*, for example, was first thought to feed on roots of dead, decaying hosts but was later shown to girdle roots of living plants (46). In categorizing the study species by host condition, I used the consensus opinion where there were multiple published accounts; however, where opinions differed I adopted the view of the most recent study, the most thorough investigation, or that of publications that summarize earlier literature on host associations (e.g. 11, 15, 37–41, 138).

I have sorted the study species into four categories based on the condition of the larval host plant at the time of colonization (see Table 1 for species and

Table 1 Cerambycid species used in discussions and data analysis^a

Subfamily	Tribe	Genus	Host condition	Larval host tissue	References
Anop.	Anoplodermini	<i>Migdolus fryanus</i> Westwood	HH	Root	12, 59, 92a
Asem.	Asemmini	<i>Arhopalus ferus</i> (Mulsant)	DH	Subcortical	11, 78, 151
Asem.	Asemmini	<i>Tetropium cinnamopterus</i> Kirby	SH	Subcortical	124
Asem.	Asemmini	<i>Tetropium gabrieli</i> Weise	SH	Subcortical	31
Asem.	Asemmini	<i>Tetropium parvulum</i> (Csy.)	SH	Subcortical	118
Asem.	Asemmini	<i>Tetropium velutinum</i> Leconte	SH	Subcortical	123
Cer.	Callichromini	<i>Aromia moschata</i> (L.)	WH	Subcortical	36
Cer.	Callichromini	<i>Callichroma velutinum</i> (F.)	SH	Subcortical	39
Cer.	Callidiini	<i>Hylotrupes bajulus</i> (L.)	DH	Wood	23, 42, 74
Cer.	Callidiini	<i>Samanotus japonicus</i> (Lacordaire)	WH	Subcortical	49, 88, 130, 131
Cer.	Callidiini	<i>Semanotus litigious</i> (Csy.)	SH	Subcortical	160
Cer.	Cerambycini	<i>Aeolesthes sarta</i> (Solsky)	WH	Wood	41, 142, 143
Cer.	Cerambycini	<i>Hoplocerambyx spinicornis</i> (New.)	SH	Subcortical	9, 40
Cer.	Cerambycini	<i>Nadezhdiella cantori</i> (Hope)	HH	Subcortical	41, 94
Cer.	Clytini	<i>Chlorophorus varius</i> Mull.	WH	Wood	11, 38, 146
Cer.	Clytini	<i>Megacyllene caryae</i> (Gahan)	SH	Subcortical	43, 58
Cer.	Clytini	<i>Megacyllene robiniae</i> (Forst.)	WH	Subcortical	68, 125, 138
Cer.	Clytini	<i>Xylotrechus pyrrhoderus</i> Bates	HH	Subcortical	83, 84, 84a
Cer.	Clytini	<i>Xylotrechus quadripes</i> Chevrolat	WH	Subcortical	41
Cer.	Elaphidiini	<i>Enaphalodes rufulus</i> (Hald.)	WH	Subcortical	34, 70, 138
Cer.	Hesperophanini	<i>Stromatium barbatum</i> (F.)	DH	Wood	9
Cer.	Methiini	<i>Styloxus bicolor</i> (Cham. & Knull)	HH	Stemwood	82
Cer.	Obrini	<i>Obrium cantharinum</i> (L.)	DH	Subcortical	11, 141
Cer.	Oemini	<i>Xystrocera globosa</i> (Oliv.)	SH	Subcortical	85
Cer.	Phoracanthini	<i>Epithora dorsalis</i> MacLeay	SH	Subcortical	6, 40
Cer.	Phoracanthini	<i>Phoracantha semipunctata</i> (F.)	SH	Subcortical	11, 64–66
Cer.	Trachyderini	<i>Tragidion armatum</i> LeConte	HH	Stem	26
Lam.	Acanthocinini	<i>Dectes sayi</i> Dill. & Dill.	HH	Stem	115
Lam.	Acanthocinini	<i>Dectes texanus</i> LeConte	HH	Stem	69, 110
Lam.	Batocerini	<i>Apriona germari</i> (Hope)	HH	Wood	41
Lam.	Dorcaschematini	<i>Dorcaschema wildii</i> Uhler	WH	Subcortical	134, 138
Lam.	Dorcaschematini	<i>Olenecamptus bilobus</i> (F.)	SH	Subcortical	41, 86
Lam.	Gleneini	<i>Paraglenea fortunei</i> Saunders	HH	Wood	155, 157
Lam.	Hippopsini	<i>Hippopsis lemniscata</i> (F.)	HH	Stem	114
Lam.	Monochamini	<i>Acalolepta luxuriosa</i> Bates	WH	Wood	4
Lam.	Monochamini	<i>Acalolepta vastator</i> (New.)	WH	Wood	41, 56, 57
Lam.	Monochamini	<i>Anoplophora chinensis</i> (Forster)	HH	Wood	41, 93, 154
Lam.	Monochamini	<i>Anoplophora glabripennis</i> (Mots.)	WH	Subcortical	62, Pers. Obs.
Lam.	Monochamini	<i>Anoplophora malasiaca</i> Thomson	HH	Subcortical	2, 3
Lam.	Monochamini	<i>Celosterna scabrator</i> (F.)	WH	Pith	8, 9, 41
Lam.	Monochamini	<i>Dihammus cervinus</i> (Hope)	HH	Wood	9, 41
Lam.	Monochamini	<i>Goes pulcher</i> (Hald.)	HH	Wood	136, 138
Lam.	Monochamini	<i>Goes pulverulentus</i> (Hald.)	WH	Wood	135, 138
Lam.	Monochamini	<i>Goes tessellatus</i> (Hald.)	HH	Sapwood	21, 138
Lam.	Monochamini	<i>Goes tigrinus</i> (DeGeer)	WH	Wood	139
Lam.	Monochamini	<i>Monochamus alternatus</i> Hope	SH	Subcortical	48, 89, 95
Lam.	Monochamini	<i>Monochamus carolinensis</i> (Oliv.)	SH	Subcortical	45, 94a, 152
Lam.	Monochamini	<i>Monochamus leuconotus</i> (Pasc.)	WH	Subcortical	32, 38, 147
Lam.	Monochamini	<i>Monochamus scutellatus</i> (Say)	SH	Subcortical	80, 81, 122
Lam.	Monochamini	<i>Neoptychodes trilineatus</i> (L.)	WH	Subcortical	77, 138
Lam.	Monochamini	<i>Plectrodera scalator</i> (F.)	WH	Root	138
Lam.	Monochamini	<i>Psaecotha hilaris</i> (Pasc.)	WH	Subcortical	52, 81b, 162
Lam.	Onciderini	<i>Oncideres cingulata</i> (Say)	HH	Stemwood	5, 14, 121, 138

(Continued)

Table 1 (Continued)

Subfamily	Tribe	Genus	Host condition	Larval host tissue	References
Lam.	Onciderini	<i>Oncideres rhodosticta</i> Bates	HH	Stemwood	116, 138
Lam.	Phytoecini	<i>Dirphyia nigricornis</i> (Oliv.)	WH	Pith	38, 159
Lam.	Phytoecini	<i>Mecas cana</i> (LeConte)	HH	Stem	144
Lam.	Phytoecini	<i>Oberea brevis</i> (Swed.)	HH	Stemwood	54, 132
Lam.	Phytoecini	<i>Oberea erythrocephala</i> (Schrank)	HH	Stemwood	129
Lam.	Phytoecini	<i>Oberea schaumii</i> (LeConte)	HH	Stemwood	81a, 107, 138
Lam.	Phytoecini	<i>Phytoecia rufiventris</i> Gautier	HH	Stem	153, 156
Lam.	Saperdini	<i>Anaerea carcharias</i> (L.)	HH	Subcortical	74, 120
Lam.	Saperdini	<i>Nupserha vexator</i> (Pasc.)	HH	Stem	144
Lam.	Saperdini	<i>Saperda calcarata</i> Say	WH	Subcortical	76, 104, 113, 138
Lam.	Saperdini	<i>Saperda candida</i> F.	HH	Subcortical	7, 19, 72, 138
Lam.	Saperdini	<i>Saperda cretata</i> New.	HH	Subcortical	20, 138
Lam.	Saperdini	<i>Saperda inornata</i> SAY	HH	Subcortical	81a, 106, 138
Lam.	Saperdini	<i>Saperda populnea</i> (L.)	HH	Subcortical	53, 109
Lam.	Saperdini	<i>Saperda tridentata</i> Oliv.	WH	Subcortical	111, 138
Lam.	Sternotomini	<i>Sternotomis pulchra</i> Drury	SH	Subcortical	38
Lam.	Tetraopini	<i>Tetraopes tetraophthalmus</i> (Forst.)	HH	Root	25, 55, 99
Lep.	Lepturini	<i>Stenurella melanura</i> (L.)	DH	Wood	11, 91, 100
Lep.	Rhagiini	<i>Gaurotes virginea</i> (L.)	SH	Subcortical	11, 140
Lep.	Rhagiini	<i>Rhagium inquisitor</i> (L.)	DH	Subcortical	11, 73
Pri.	Anacolini	<i>Prionoplus reticularis</i> White	DH	Subcortical	40, 44
Pri.	Ergatini	<i>Ergates faber</i> (L.)	DH	Wood	15, 37, 74
Pri.	Prionini	<i>Dorysthenes forficatus</i> (F.)	HH	Root	38
Pri.	Prionini	<i>Dorysthenes hugeli</i> Redtenbacher	HH	Root	41
Pri.	Prionini	<i>Prionus californicus</i> Mots.	HH	Root	16, 138
Pri.	Prionini	<i>Prionus coriarius</i> (L.)	DH	Root	11, 35
Pri.	Prionini	<i>Prionus imbricornis</i> (L.)	WH	Root	138, 145
Pri.	Prionini	<i>Prionus laticollis</i> (Drury)	WH	Root	10, 46, 47, 138

^aAbbreviations: HH, healthy host; WH, weakened host; SH, stressed host; DH, dead host

references). These categories are similar to those that Wood (161) used in categorizing bark beetle species by larval host condition. The categories are:

1. Healthy host (HH) species are those that oviposit only on host plants that are vigorous. Among these are species whose larvae feed in the stems of herbaceous plants (Table 1: host tissue labeled “stem”), in twigs and branchlets of woody plants (host tissue labeled “stemwood”), or cause woody plants to form a gall-like structure (lamiines *Dihammus cervinus*, *Saperda cretata*, *S. inornata*, *S. populnea*). Also included are species in which the adult females girdle the stems of herbaceous plants or branches of woody hosts prior to oviposition (lamiines *Mecas cana*, *Oberea brevis*, *Oberea erythrocephala*, *Oncideres cingulata*, *Oncideres rhodosticta*, *Phytoecia rufiventris*), or the larvae internally girdle branches of herbaceous and woody plants (lamiines *Dectes texanus*, *Nupserha vexator*; cerambycine *Styloxus bicolor*), or girdle and sever roots (prionines *Dorysthenes hugeli*, *P. californicus*; anoplodermine *Migdolus fryanus*). HH species require living hosts, and larvae may not

be able to complete development if the host dies (lamiines *Saperda candida*, *S. inornata*). Many species apparently never kill their host plant (lamiines *Dectes sayi*, *D. cervinus*, *Hippopsis lemniscata*, *O. brevis*, *O. schaumii*, *S. inornata*, *T. tetraophthalmus*); however, larvae of other species may occasionally weaken the host to a fatal degree (lamiines *Anoplophora chinensis*, *A. malasiaca*, *Apriona germari*, *D. texanus*, *Goes tessellatus*, *S. cretata*, *S. inornata*, and cerambycine *Nadezhdiella cantori*).

2. Weakened host (WH) species attack host plants that are alive and growing, but whose defenses have been compromised in some way, such as by chronically poor growing conditions (soil compaction, low soil nutrients, drought; *Megacyllene robiniae*), flooding (*Goes tigrinus*), moderate fire damage (*M. robiniae*), or attack by other insects, including earlier generations of borers. Poor growing conditions may render trees in urban habitats more prone to attack by WH species than are those growing in natural habitats (*Aeolesthes sarta*, *Saperda tridentata*). In many cases, cerambycid species thought to attack living, healthy trees have later been found to depend on hosts being weakened in some way (e.g. compare reference 97 with references in Table 1 for *Saperda calcarata*, *S. tridentata*, *M. robiniae*). For that reason, I include in the WH category species that are recorded as attacking both healthy and weakened trees (e.g. *A. glabripennis*, *Enaphalodes rufulus*, *Goes pulverulentus*, *G. tigrinus*, *Plectrodera scalator*).

The key criterion of the WH category is that the weakened condition of the host plant is sublethal; hosts may survive for years despite harboring borer larvae. Larval feeding may contribute to decline of hosts, particularly when they are repeatedly attacked by multiple borer generations (lamiines *Dorcashema wildii*, *Goes pulverulentus*, *G. tigrinus*, *Neoptychodes trilineatus*, *S. calcarata*, *S. tridentata*; cerambycine *A. sarta*). Ultimately, the host plant may die (lamiines *Anoplophora glabripennis*, *Celosterna scabrator*, *D. wildii*, *Monochamus leuconotus*, *N. trilineatus*, *S. tridentata*; cerambycines *A. sarta*, *Chlorophorus varius*); however, many species rarely kill the host (lamiines *P. scalator*, *S. calcarata*; cerambycines *M. robiniae*, *Semanotus japonicus*, *Xylotrechus quadripes*), or never do (lamiine *Psa-cothea hilaris*). Some species are incapable of completing development in dead hosts (lamiine *P. hilaris*; cerambycine *E. rufulus*).

3. Stressed host (SH) species attack woody plants that are severely stressed, often to the point that death is imminent, such as by drought (*Phoracantha semipunctata*), and attack by other organisms, especially bark beetles (*Megacyllene caryae*; 28) and nematodes (95). A common trait of SH species is that they will oviposit on, and may indeed show an oviposition preference for, freshly felled trees and cut logs. The key criterion of the SH category

is that hosts usually die, often as a direct result of larval colonization, and support only a single generation of SH species, later becoming infested with species that are restricted to dead hosts (e.g. 60, 127).

4. Dead host (DH) species require woody plants that are no longer green, and may be dry and seasoned or decaying, moist, and riddled with fungal hyphae. Hosts of these species commonly support several generations of borers (e.g. asemine *Arhopalus fesus*, lepturine *Rhagium inquisitor*).

Larval Host Tissues

NUTRITIONAL QUALITY Tissues of woody plants vary in the following ways in their nutritional quality for wood-boring insects (29, 60, 63, 79, 127): (a) bark is generally very low in nutrients (carbohydrates, nitrogen); (b) subcortical zone tissues (inner bark, cambium, immature xylem) have many times higher concentrations of nutrients; (c) the much thicker sapwood is low in nutritional quality; (d) the quality of heartwood is lower still; (e) pith has a somewhat higher nitrogen content than heartwood. The nutritional quality of both sapwood and heartwood in dead woody plants may be greatly improved by proliferation of fungal hyphae, which may favor development of wood borers (60, 74, 127). Larvae of species that feed in nutrient-deficient tissues such as dry, seasoned wood, however, may depend on cellulose-digesting enzymes to assist in nutrient assimilation (e.g. 102).

Reflecting relative nutritional quality of woody tissues, the greatest diversity of wood-feeding insects confine their feeding to subcortical tissues, and few species feed within the wood (127). Among the study species (Table 1), most feed subcortically at least initially. Larvae of many HH and WH species, however, feed relatively briefly under bark, spending most of their developmental period in the sapwood or heartwood (e.g. *A. malasiaca*, *Anaerea carcharias*, *Goes pulcher*, *G. pulverulentus*, *M. leuconotus*, *M. robiniae*). SH species feed nearly exclusively within the subcortical zone and may score the sapwood, but only enter it to pupate; larvae may resort to feeding in sapwood once the cambium has been completely consumed or the bark becomes thin (LM Hanks, personal observation). *Monochamus* larvae may feed subcortically for several weeks, then burrow into the sapwood, but return to the cambial zone to continue feeding (e.g. *Monochamus carolinensis*; 112); however, they may not consume sapwood tissues while burrowing (127).

Many DH species also feed subcortically; others feed within the sapwood and may only resort to consuming heartwood when sapwood has been decimated (e.g. *Prionoplus reticularis*, *Hylotrupes bajulus*; 74).

AVAILABILITY AND PREDICTABILITY OF HOST TISSUES Most cerambycid species require host plants whose resistance mechanisms have been compromised in some way (105). Girdling of plant parts by lamiine adults manipulates

the condition of the host tissues, rendering a healthy branch, stem, or root stressed or moribund. Girdling may circumvent host resistance by, for instance, preventing the flow of sap (e.g. *Sthenias grisator* [F.] in 41), but may also elevate nitrogen content in the girdled portion owing to pooling of amino acids (51). That girdling renders branches suitable for colonization by wood borers in general is shown by secondary infestation of girdled branches by a wide variety of nongirdling species, including cerambycids and bostrichids (e.g. 33, 116, 121). For species that girdle host plants, the larval host is a relatively stable and predictable resource because the beetles need not depend on hosts being in any particular condition, but rather any living host may provide suitable breeding material. The same is true for other species whose larvae feed in healthy hosts.

WH species, by definition, prefer weakened hosts; plant resistance has been attributed to high moisture content of bark (*A. glabripennis*; 117) or sapwood (*Acalolepta vastator*, *G. tigrinus*), sap or resin flow (lamiines *G. pulverulentus*, *S. calcarata*; cerambycines *E. rufulus*, *S. japonicus*), secondary chemicals (*A. glabripennis*; 158), and undetermined factors (lamiines *A. carcharias*, *C. scabrator*, *N. trilineatus*; cerambycine *M. robiniae*). Although WH species require hosts in a particular condition, their larval resources are nevertheless relatively stable and persistent because hosts remain for long periods in a condition suitable for larval colonization. In fact, it is this stability that allows re-infestation of hosts by multiple generations of borers (see above).

Colonization of subcortical tissues by SH species requires that hosts be severely stressed, such as is the case with a freshly fallen branch or a tree attacked by bark beetles. There is a distinction between such stressed hosts and dead hosts: For example, a tree that has been recently felled is not dead because cellular metabolism continues for a period; nevertheless, it is doomed. Resistance of host plants to SH species has been attributed to high bark turgor pressure (*P. semipunctata*; 24), high bark moisture content (asemine *Tetropium gabrieli*; cerambycine *Epithora dorsalis*, *P. semipunctata*), and sap or resin flow (cerambycine *Hoplocerambyx spinicornis*, lamiine *Sternotomis pulchra*). Once resistance is lost, prime subcortical tissues are usually rapidly invaded by subcortically feeding insects (60, 63, 127). Rapid degradation of subcortical tissues explains why SH species are attracted to individual hosts for only a short period (e.g. 67). Hosts of SH species also become available sporadically, such as from wind damage, lightning strike, forest fire, drought, or bark beetle attack. Thus, subcortical tissues of a stressed or dying tree are an ephemeral and unpredictable resource, but at the same time represent the highest-quality food resource and the smallest volume of woody tissues. These resource qualities are responsible for extreme intra- and interspecific scramble competition among wood borers for subcortical tissues of dying trees (e.g. 67); this competition results in high rates of larval mortality in SH species, which accounts

for a significant portion of the total generational mortality (*P. semipunctata*, *Monochamus alternatus*, *M. carolinensis*, *M. scutellatus*).

Like those of HH and WH species, larval resources of DH hosts are relatively stable because dead wood may vary little in nutritional quality over long periods, and decomposition of wood is a prolonged process (e.g. 127). Stability of dead hosts as a larval resource is illustrated by their being attacked by multiple generations of borers (see above).

Host Location and Oviposition

Choice of oviposition hosts by adult female cerambycids is critical because the larvae are usually legless and incapable of moving between hosts. Even root-feeding larvae (prionines, *Tetraopes* species) are probably limited in the distance they can travel through the soil in search of hosts (e.g. 55). Adult cerambycids locate suitable larval hosts by olfaction (97). For example, adult timber beetles (*Monochamus* species; SH) are attracted by pine terpenoids, monoterpenes, and ethanol (e.g. 27); volatiles of freshly cut trees (e.g. 75); and semiochemicals of bark beetles that kill conifers (13). Species that attack nonconiferous plants show similar attraction to host plant volatiles (cerambycines *P. semipunctata*, *H. spinicornis*).

Adult lamiines are unique among cerambycids in gnawing an egg niche into bark or stems (37, 97) and covering eggs with a material from the ovipositor, which hardens (many species in Table 1). Females of other subfamilies typically wander over the host, probing the bark with the ovipositor for appropriately sized cracks and crevices in which they oviposit (lepturine *R. inquisitor*; cerambycines *H. bajulus*, *N. cantori*, *P. semipunctata*, *Xystrocera globosa*). Among the study species, lamiines deposit an average of 2.1 ± 0.6 ($N = 25$) eggs per niche, cerambycines deposit eggs in batches of 9.5 ± 4.7 eggs ($N = 12$), and prionines in groups of 9.8 ± 4.3 ($N = 6$; means significantly different, ANOVA $F = 3.1$, $P < 0.05$). Incubation times were shorter in SH species (mean = 10.7 ± 1.3 days, $N = 13$) than in HH (mean = 13.8 ± 1.5 days, $N = 25$), WH (mean = 14.3 ± 1.9 days, $N = 15$), and DH species (mean = 18.0 ± 2.7 days, $N = 8$; means not significantly different, ANOVA $F = 1.84$, $P > 0.05$). Incubation period varied significantly among subfamilies, being longer in prionines (24.5 ± 2.7 days, $N = 8$) than in cerambycines (12.7 ± 1.8 days, $N = 30$) or lamiines (10.9 ± 1.3 days, $N = 16$; ANOVA $F = 14.4$, $P < 0.0001$).

Adult Diet

Although adults of many cerambycid species mate immediately after emergence, lamiines appear to require a period of maturation feeding (97); lamiine study species feed for an average of 6.7 ± 1.2 days ($N = 21$) before mating compared with 0.17 ± 0.17 days ($N = 6$) for cerambycines (means

significantly different, ANOVA $F = 7.7$, $P = 0.01$). In addition, the period between adult emergence and oviposition was more than twice as long in lamiines than in cerambycines; 9.0 ± 1.0 days ($N = 24$) compared with 4.2 ± 1.4 days ($N = 7$; means significantly different, ANOVA $F = 5.64$, $P = 0.024$). Neither precopulatory nor preoviposition period varied significantly among species in the HH, WH, and SH categories (ANOVA $P > 0.05$).

Adult cerambycids feed on foliage (mostly lamiine species), conifer needles (*Monochamus* species), tender bark of stems and shoots (mostly lamiines), floral resources (lepturines and many cerambycines), or seeping sap (mostly cerambycines; 37, 97). Adults of some species, however, do not feed at all; these can be found in all of the host condition categories except SH. The lack of feeding appears to be most prevalent among root and dead-wood feeders. Root feeders include prionines *Dorysthenes forficatus* (an HH species), *D. hugeli* (HH), *Prionus coriarius* (DH), *P. laticollis* (WH), and anoplodermine *M. fryanus* (HH); dead-wood feeders include prionines *P. reticularis* and *Ergates faber* (in decaying hosts), asemine *A. fesus* (in dead hosts), and cerambycines *H. bajulus* and *Stromatium barbatum* (in seasoned wood). Other HH species with adults that appear not to feed are the vine-boring cerambycine *Xylotrechus pyrrhoderus* and *S. bicolor*, whose larvae internally girdle branches. Absence of feeding in the adult stage of many species is associated with the production of long-range pheromones (see *Mate Location and Recognition*).

Not surprisingly, adult cerambycids that do not feed have shorter longevities than those that do; 4.0 ± 2.7 days ($N = 9$) compared with 36–53 days in species that feed on bark ($N = 14$), foliage ($N = 43$), floral resources ($N = 4$), or stems of herbaceous plants ($N = 5$; means significantly different, ANOVA $F = 3.92$, $P = 0.0089$).

Adult Dispersal

Shibata (131) has suggested that dispersal activity of two species of Japanese cerambycids, *S. japonicus* and *M. alternatus*, is dependent on the association between dietary requirements of adults and host condition requirements of the larvae. This pattern is also evident among other cerambycid species. Adults of lamiine HH species, for example, have the option of feeding on plant individuals that are also suitable hosts for their larvae; adults may feed on bark or foliage of woody plants, or stems of herbaceous hosts. Adults of WH lamiine species are also able to feed on the same host individuals on which they may oviposit, and also feed on bark and foliage. The proximity of adult feeding/mating sites and oviposition sites for HH and WH species accounts for the relatively sedentary nature (i.e. a disinclination to take flight and disperse) in adults of both sexes (lamiines *A. glabripennis*, *D. sayi*, *D. texanus*, *D. cervinus*, *G. tessellatus*, *H. lemniscata*, *S. candida*, *S. inornata*, *T. tetraophthalmus*; cerambycines

N. cantori, *S. japonicus*), or at least adult females (lamiines *A. vastator*, *A. chinensis*, *A. malasiaca*, *M. leuconotus*). Female WH species may even oviposit on their natal host if its health has not declined too greatly (see above); this behavior results in a contagious distribution (57, 76). In contrast to these sedentary species, adults of other HH and WH species appear to be rather active and include (a) cerambycine species that may benefit from strong powers of dispersal because adults feed on host plant species different from the larval host (*M. robiniae*, *Aromia moschata*, *C. varius*); (b) lamiine species that would not appear to benefit from high vagility because adults feed on bark or leaves of woody larval hosts (*C. scabrator*) or stems or leaves of herbaceous hosts (*M. cana*, *N. vexator*, *O. brevis*). Regardless of the general level of activity, males are usually more active than females (lamiines *A. vastator*, *A. carcharias*, *A. chinensis*, *A. malasiaca*, *D. cervinus*, *M. leuconotus*, *O. erythrocephala*, *Oberea schaumii*, *Paraglenea fortunei*, *P. hilaris*, *S. candida*, *T. tetraophthalmus*; cerambycines *A. moschata*, *S. japonicus*).

Adults of SH species usually must seek healthy hosts for their own feeding, and therefore do not share individual hosts with their progeny; adults may feed on the bark, foliage, or flowers of the same species as the larval host, but different host individuals (cerambycines *H. spinicornis*, *P. semipunctata*; lamiines *Olenecamptus bilobus* and many *Monochamus* species; 95), or flowers of entirely different plant species (cerambycine *M. caryae*; lepturine *Gaurotes virginea*). Both sexes aggregate on the larval host where mating takes place. Strong dispersal abilities described for SH species (lamiine *M. alternatus*; cerambycines *M. caryae*, *H. spinicornis*, *P. semipunctata*) are adaptive because adults must disperse alternately between their food plants and the stressed host plants where they mate and oviposit (see 63).

Like SH species, adults of DH species feed on plants that are not suitable hosts for larval development. Strong dispersal powers are shown by adults that feed on flowers (cerambycine *Obrium cantharinum*). Elimination of adult feeding in prionines and anoplodermine species greatly reduces the need to disperse long distances regularly, and adults are reportedly relatively sedentary (*P. reticularis*, *P. laticollis*), females do not disperse readily (*D. forficatus*, *P. imbricornis*) or are apterous (*M. fryanus*, *P. laticollis*). Nevertheless, adult asemine *A. ferus* and cerambycine *H. bajulus* do not feed but are relatively strong dispersers. Dispersal may be adaptive in locating new larval hosts and avoiding inbreeding.

Mate Location and Recognition

For most cerambycids, adult males usually play the active role in mate location (97). It has long been held that these beetles, like most other insects, depend on pheromones that act over long distances for mate location (e.g. 97); however,

convincing evidence of long-range pheromones in the cerambycids has been limited to a very few species in the HH, WH, and DH categories, and is often coincident with the lack of feeding in the adult stage and sedentary behavior in the pheromone-producing sex. Pheromones that operate over at least moderate distances (~ 1 m) are produced by females of the root-feeding anoplodermine *M. fryanus* (12, 92a), males of the dry-wood feeder *H. bajulus* (50), and of the vine-boring *X. pyrrhoderus* (84a). Such pheromones are also suspected in male *Xylotrechus chinensis* and female *S. bicolor* (82), both cerambycines, and females of the dead wood-feeding prionine *P. reticularis* (44). Other prionine species also show behaviors that implicate pheromones (*P. laticollis*; 61, 133), and the lack of flight in females of some species (*P. imbricornis*) and absence of feeding in others (*D. forficatus*, *D. hugeli*, *E. faber*, *P. coriarius*) suggest that pheromones may be involved in mate location.

For cerambycid species that feed in the adult stage, mate location behavior is associated with larval host condition. Males of HH and WH species, for example, often seek females at the adult feeding site, which is also the larval host (lamiines *A. carcharias*, *A. chinensis*, *A. glabripennis*, *A. malasiaca*, *O. erythrocephala*, *O. schaumii*, *P. scalator*, *S. candida*, *P. hilaris*; cerambycines *S. japonicus*, *X. pyrrhoderus*) or flowers of different species (cerambycines *A. moschata*, *M. robiniae*). In some lamiine species, the male may remain near or mounted on his mate while she girdles the host branch or prepares the egg niche (*A. glabripennis*, *G. pulverulentus*, *O. cingulata*, *P. rufiventris*). In most species, however, the female usually oviposits alone.

Careful observation of many HH and WH species (all lamiines) has revealed that long-range pheromones are not involved in mate location (*A. vastator*, *A. chinensis*, *O. erythrocephala*, *O. schaumii*, *P. fortunei*, *P. rufiventris*, *S. inornata*, *S. populnea*); an inability to detect mates at long distances has also been reported for *Oberea oculata* L. (53). Mate location appears to depend on males encountering females by chance (lamiines *A. chinensis*, *O. erythrocephala*, *O. schaumii*, *S. inornata*, *S. populnea*; cerambycines *N. cantori*, *Tragidion armatum*), and males recognizing females by antennal contact (lamiines *A. chinensis*, *P. rufiventris*, *P. hilaris*; cerambycine *M. robiniae*), by very short-range pheromones operating over distances of a few centimeters (lamiines *P. hilaris*, *P. fortunei*; cerambycine *S. japonicus*), or visually over similarly short distances (*P. rufiventris*). The probability of encountering a mate by chance on adult host plants, and hence mating opportunity, would seem to be very low, particularly on large host trees. Adults of some species, however, appear to improve their chances of encountering mates by seeking individual hosts of a particular type. For example, adults of *M. robiniae* prefer to visit goldenrod plants that are most conspicuous because they are isolated and have larger and brighter inflorescences (68), *T. tetraophthalmus* tends to aggregate on certain milkweed plants

(though the cue for aggregation is not known; 25), adult *A. malasiaca* also show contagious distributions among host trees (3), and preference in *P. rufiventris* adults for tall host plants for feeding tends to bring the sexes together (153).

Studies of SH species have also suggested the absence of long-range pheromones (cerambycine *P. semipunctata*; lamiines *M. alternatus*, *M. carolinensis*, *M. scutellatus*; 95). In these species, mate location apparently depends on mutual attraction to the larval host where males rely on antennal contact to recognize females. Although Fauziah et al (48) suggest that male *M. alternatus* produce a long-range pheromone, and Kim et al (87) reported evidence of pheromones in laboratory bioassays, field observations of Okomoto (108) revealed that both sexes are independently attracted to the larval host where males locate females solely by antennal contact.

Adult females and males of some DH species may encounter one another on the adult food plant (flowers or leaves of plants other than the larval host; cerambycines *O. cantharinum*; lepturines *Stenurella melanura*, *R. inquisitor*). Michelsen (101) and Heintze (71) concluded that mate recognition in most lepturine species and flower-feeding cerambycines is accomplished by antennal contact on the adult host. However, many DH species that do not feed as adults apparently use long-range pheromones in mate location, as has been already discussed. As with HH and WH species, DH females usually oviposit alone.

Mate Location and Antennal Morphology

Pheromones that act over long distances appear to be rather rare in the Cerambycidae, a circumstance that correlates well with antennal morphology. Sensitivity to long-range pheromones in other insects is enhanced by increasing the surface area of the antennae (and hence the abundance of olfactory sensilla), leading to the evolution of branched antennae that are lamellate, pectinate, serrate, etc (128). Such branched antennal morphologies are indeed evident in males of many prionine species (97), some of which apparently rely on pheromones for mate location (see above *Mate Location and Recognition*). Other cerambycid species that use long-range pheromones (*H. bajulus*, *M. fryanus*, *X. pyrrhoderus*) have antennae that are relatively short, like those of the prionines, but differ little in structure between the sexes. An exception is the cerambycine *S. bicolor*, which is believed to use pheromones (82), but males have long, filamentous antennae (98).

The majority of cerambycids have antennae that are nearly filiform, but relatively elongate (18), a structure not especially well suited for sensitivity to long-range pheromones (128). Blatchley (17) speculated that the elongate antennae of cerambycids provide balance when walking on slender twigs, as a pole does for a tightrope walker. Other authors have not speculated on the adaptive significance of elongate antennae in cerambycids, but sexual dimorphism

in length has been taken as evidence that they play a role in mate location (96, 119). Behaviors shown by the study species, however, suggest that males of many HH, WH, and SH species depend on antennal contact to locate and recognize mates (see *Mate Location and Recognition*, above). Elongate antennae may be especially advantageous for SH species, which mate on the larvae hosts where males seek females by antennal contact. Males of *M. alternatus* and *P. semipunctata* search for females by splaying the antennae and skimming the bark surface (65, 108). In these species, as in others, elongation of the male antennae (two or more times the body length) may impart a significant fitness advantage by improving their efficiency in locating mates (65).

Mating Behavior

Cerambycids appear to be consistent in not showing any form of precopulatory courtship behavior; males typically approach females directly and attempt to mount and copulate (lepturine *S. melanura*; cerambycines *A. moschata*, *E. dorsalis*, *N. cantori*, *Semanotus litigiosus*, *S. bicolor*, *X. pyrrhoderus*; laminiines *D. sayi*, *H. lemniscata*, *M. alternatus*, *M. carolinensis*, *M. scutellatus*, *O. schaumii*, *P. scalator*, *S. candida*, *S. inornata*, *S. populnea*, *S. pulchra*).

Refractoriness in females appears to be most pronounced in nonfeeding species (prionines *P. coriarius*, *P. laticollis*; cerambycine *H. bajulus*), perhaps reflecting their short life span and brief opportunity to oviposit. Duration of copulation varies greatly among cerambycids, being similarly prolonged in HH and WH species (61.7 ± 14 and 42.9 ± 20 min, respectively), but very brief in SH species (0.87 ± 0.53 min; means significantly different, Kruskal-Wallis statistic = 17.6, $P = 0.0002$). Thus, for species in which females often oviposit alone (many HH, WH, and DH species), pairs spend much of their bonding period *in copula* (females may feed during this time). Prolonged mating is necessary for complete fertilization in *C. varius*, *Dirphya nigricornis*, and *P. hilaris*, and a single copulation is sufficient to fertilize all of the eggs of female *S. inornata*, *H. bajulus*, *O. schaumii*, and *X. pyrrhoderus*.

Although copulation of SH species is very brief, the male remains with the female as she searches for oviposition sites, repeating copulation and fending off rival males. Repeated mating is necessary for *Acalolepta luxuriosa* and *X. globosa* females to realize fully their potential fecundity. *M. alternatus* females, however, need only mate once for complete fertilization, and the advantages of pair-bonding for females are unclear. Pair-bonding does, however, favor male *M. scutellatus* because eggs are fertilized by the most recent mating, assuring paternity of eggs oviposited while the male attends his mate. Mate defense is critical for some SH species because sex ratios of adults on the larval hosts are often strongly male-biased (*P. semipunctata*, *M. caryae*).

DISCUSSION

To some extent, variation in reproductive behavior among cerambycid species can be attributed to taxonomic affiliation. An example is the lamiines, all of which seem to require maturation feeding and usually feed on the same host species as do their larvae, regardless of larval host species condition. Lamiine species that attack living and healthy or weakened hosts (HH and WH species) are essentially homogeneous in their behaviors, with adults often feeding, mating, and ovipositing on the same host individual (tribes Phytoecini, Saperdini, but also *Dectes* species, *Oncideres* species, *A. germari*, *D. wildii*, *P. fortunei*, *H. lemniscata*, and several species of Monochamini). Categorizing many of these species by larval host condition appears to be rather arbitrary, particularly species that girdle stems of herbaceous plants or branches of woody plants (*M. cana*, *O. brevis*, *O. erythrocephala*, *O. cingulata*, *O. rhodosticta*, *P. rufiventris*). By girdling, the adult female weakens a part of her healthy host for the benefit of the larvae. These species are therefore ecologically more closely affiliated with WH species than HH species. Closer inspection of other putatively HH lamiine species has revealed that they nevertheless may require that hosts be somewhat less than vigorous; For example, larvae may be more abundant in hosts that are moisture stressed (*O. cingulata*; 5); mortality may be higher in healthy hosts (*A. carcharias*), in some cases due to diminished sap flow (*O. cingulata*, *G. pulcher*), or unidentified resistance factors (*S. inornata*). Thus, the line separating lamiine HH and WH species is blurred.

The few cerambycine study species (of several tribes) that attack living or weakened hosts (WH and HH species in Table 1) show important differences with the lamiines; adults do not feed on larval hosts but rather feed on flowers of other species (*A. moschata*, *C. varius*, *M. robiniae*), or may not feed at all (*S. bicolor*, *X. pyrrhoderus*). Among the species that feed as adults, the need to disperse between adult and larval hosts is reflected in the active nature of at least some of these species (*A. moschata*, *M. robiniae*), in contrast to the relatively sedentary nature of many of the HH and WH lamiines.

Although differences in behavior among HH and WH species appear to fall largely along subfamily lines, SH species show convergent behaviors across subfamilies. Behaviors of lamiine, cerambycine, and asemine species that exploit the subcortical tissues of stressed or dying hosts reflect the ephemeral and unpredictable qualities of the larval resource; adults of both sexes are strongly attracted to larval hosts where they aggregate and mate, copulation is brief, and incubation time of eggs is short. These behaviors would seem to expedite the placement of the larvae and are highly adaptive because the first larvae to

Table 2 Duration of copulation time for closely related cerambycid species in different categories of larval host condition (see Table 1 for references)^a

Subfamily/Tribe	Species	Host condition	Copulation time (min)
Cerambycinae			
Callichromini	<i>Aromia moschata</i> (L.)	HH	180.0
	<i>Callichroma velutinum</i> (F.)	SH	1.1
Callidiinae	<i>Semanotus japonicus</i> (Lacordaire)	HH	4.9
	<i>Semanotus litigiousus</i> (Csy.)	SH	0.17
	<i>Hylotrupes bajulus</i> (L.)	DH	4.4
Cerambycini	<i>Nadezhdiella cantori</i> (Hope)	HH	1.5
	<i>Hoplocerambyx spinicornis</i> (New.)	SH	0.05
Clytini	<i>Xylotrechus pyrrhoderus</i> Bates	HH	15.2
	<i>Chlorophorus varius</i> Mull.	WH	55.0
	<i>Megacyllene robiniae</i> (Forster)	WH	1.5
	<i>Megacyllene caryae</i> (Gahan)	SH	0.05
Lamiinae			
Monochamini	<i>Anoplophora chinensis</i> (Forst.)	HH	4.3
	<i>Celosterna scabrator</i> (F.)	WH	2.8
	<i>Psacotha hilaris</i> (Pasc.)	WH	6.5
	<i>Monochamus leuconotus</i> (Pasc.)	WH	98.0
	<i>Monochamus alternatus</i> Hope	SH	0.62
	<i>Monochamus scutellatus</i> (Say)	SH	0.33

^aAbbreviations: HH, healthy host; SH, stressed host; DH, dead host; WH, weakened host

colonize the host will have access to the best nutrition and will also have a size advantage over later competitors. The selective advantage of brief copulation time for SH species is evident in comparisons among closely related species of different host-condition categories (Table 2); all of the SH species have much briefer copulation times than closely related WH or DH species.

Deadwood feeders as a group also appear to show some consistencies in reproductive behavior beyond taxonomic classification. For example, DH species that apparently do not use long-range pheromones, such as cerambycine *O. cantharinum* and lepturines *S. melanura* and *R. inquisitor*, encounter mates on flowers where they feed. Prionines, however, which include most of the DH study species, show little variation in behavior even though their larvae utilize hosts that vary greatly in host condition; from dead wood (*P. reticularis*, *E. faber*) to roots of healthy (*D. forficatus*, *D. hugeli*), weakened (*P. laticollis*), or dead (*P. coriarius*) hosts. Nevertheless, the association in prionines between deadwood or root feeding habits in larvae and the lack of feeding in the adult stage is also evident in the asemine *A. ferus*, the anoplodermine *M. fryanus*, and the cerambycines *H. bajulus* and *S. barbatum*. Moreover, at least *M. fryanus* (12, 92b) and *H. bajulus* (50) rely on pheromones for mate location, a trait that

appears to be common among prionines. This association between the use of pheromones and the lack of feeding in the adult stage suggests that DH species that do not feed as adults (e.g. *A. ferus*, *S. barbatum*) are likely to depend on pheromones for mate location.

RESEARCH NEEDS

Information on the 81 cerambycid species discussed in this paper was from references published over a 90-year period, for an average publication rate that covered less than one species per year. This paucity of information is reflective of the rarity with which researchers and collectors record sufficient detail on the behavior of adult cerambycids. Much more could be learned of the biology and behavior of these beetles if the following information were provided in future publications: precopulation and preoviposition period, feeding behavior and dispersal behavior of adults, longevity of adult (with adult food and water provided), site where mating takes place, mechanisms of mate location and recognition, duration of mating and oviposition behaviors, fecundity and incubation period, and finally condition of the larval host. More consistent and detailed information of this type will be invaluable in providing insights into the reproductive strategies of cerambycid beetles that may be implemented in developing management strategies for the many species that are important pests as well as in comparative studies on the evolution of behavior in insects.

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