Chapter 21
Vibrational Behavior in Bark Beetles: Applied Aspects

Richard W. Hofstetter, Nicholas Aflitto, Carol L. Bedoya, Kasey Yturralde, and David D. Dunn

Abstract Acoustic signals are used for intraspecific communication in bark beetles and a variety of stridulatory mechanisms have evolved within the subfamily Scolytinae (Coleoptera: Curculionidae). Bark beetles use stridulatory signals for communication at the tree surface and within tunnels inside tree tissues. Bark beetles produce a variety of call types that are broadband with frequencies ranging from 1 to 80 kHz. Not only are airborne and substrate-borne vibrations available, but every stridulation event produces both airborne and substrate-borne vibrations via the same action of the animal. Vibrations appear to be used during species recognition, premating interactions, pair formation, mate selection, intraspecies aggression, territoriality, and predator deterrence. No sound receptors have been located for bark beetles; however, we propose potential locations in this chapter. We provide an overview of acoustic communication and its use by adult bark beetles, describe their stridulatory structures, interpret how vibrations move within tree materials and how this affects the beetles' ecology and behavior, and present technical and applied applications of acoustic tools for bark beetle management.

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21.1 Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are an ecologically and economically important subfamily of weevils that colonize tree phloem and other plant parts such as seeds and stems (Raffa et al. 2015). Over 6000 species of Scolytinae have been described (Hulcr et al. 2015) and can be found throughout the world wherever trees are located (Vega and Hofstetter 2015). Several bark beetle species are capable of altering large scale forest patterns over time via their selection of particular trees and resulting tree mortality (Eidmann 1992; Raffa et al. 2008; Bentz et al. 2010). Most bark beetle species utilize tree materials where they mate, lay eggs, and complete larval development (Raffa et al. 2015). Life history strategies can be monogamous or polygamous with regard to mating, and solitary or gregarious with regard to feeding (Kirkendall 1983; Wermelinger 2004). Bark beetles are highly adapted to life within trees and thus are adapted to boring and communicating within tree material. Adult beetles bore into phloem making cylindrical tunnels that often lack light (i.e., complete darkness) and may contain high levels of plant defensive compounds such as monoterpenes (Raffa et al. 1993). Signals from air- and substrate-borne vibrations become important once beetles are within tunnels or at the tunnel entrance (Rudinsky and Michael 1972, 1973; Ryker and Rudinsky 1976a; Swaby and Rudinsky 1976; Rudinsky et al. 1978 and many others).

Host tree selection and mate location involve chemical cues via gustation (e.g., tasting tree tissues), olfaction (e.g., detection of pheromones related to beetles within tree tissues), and possibly sound (Rudinsky and Michael 1974; Ryker 1984; Raffa et al. 2015). Acoustic cues have been proposed for host tree location (Mattson and Haack 1987), and some evidence suggests that they can hear and respond to the sounds resulting from tree cavitation in response to drought conditions (Kaiser 2014). Multimodal communication, such as chemical and acoustic are likely required to convey species-specific and individual information to conspecifics (typically of the opposite sex) within the tree (Rudinsky and Michael 1972; Rudinsky et al. 1973; Ryker et al. 1979; Birch 1984).

Bark beetles produce sound by rubbing body parts or body-substrate friction (Barr 1969; Lyal and King 1996) called stridulations (Wessel 2006). There is great diversity in the types of structures employed in stridulation by bark beetles among genera, species and between the sexes (Fig. 21.1) (Barr 1969; Ryker 1988; Lyal and King 1996; Kerchev 2015). Interestingly, stridulatory structures, regardless of the location of the body, are often sexually dimorphic and less-developed or absent in the sex that initiates tunnel construction (i.e., pioneer or colonizing sex) (Barr 1969).

Bark beetles produce a variety of call types that vary in temporal characteristics. General call types appear somewhat consistent within genera (Rudinsky and Michael 1974; Lyal and King 1996; Yturralde 2013); however, intraspecific differences occur between chirps produced in different contexts (Michael and Rudinsky 1972; Fleming et al. 2013). Signal characteristics in bark beetles show that both air- and substrate-borne vibrations are present and potentially detectable by conspecifics at distances within a few centimeters (Fleming et al. 2013), and

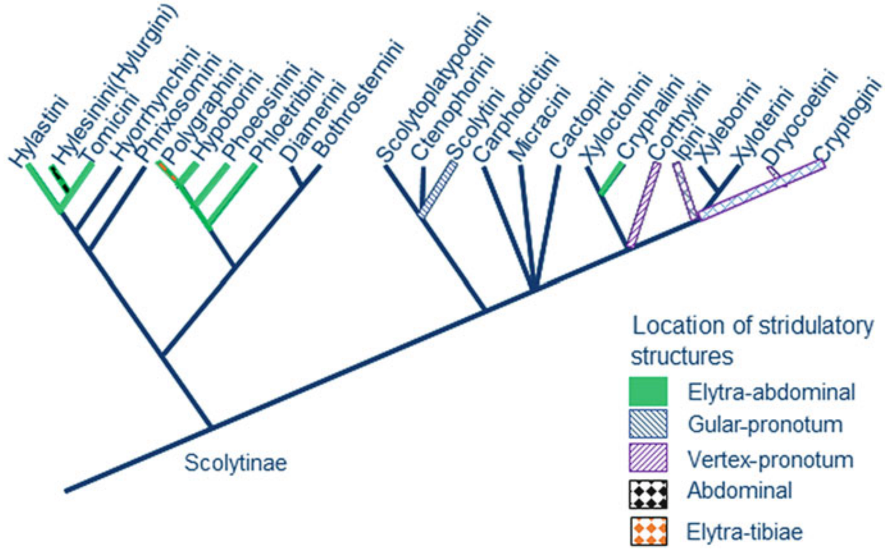

Fig. 21.1 Phylogeny of Scolytinae modified from Wood (1982) and Kirkendall (1983) and location of stridulatory structures based on review of stridulatory structures by Lyal and King (1996) and more recent publications on individual species. Some tribes have more than one stridulatory mechanism (e.g., Hylurgini, Polygraphini, and Cryptogini)

these close signals could be detected using a variety of receptors (Yack 2004, 2016). However, no sound receptors have been located for bark beetles; here, we propose potential locations.

Bark beetle acoustic communication remains one of the least studied and underappreciated forms of communication in this group of insects. Despite the ubiquity and purported importance of acoustic signals in bark beetles (Rudinsky 1969; Rudinsky and Michael 1972; Ryker 1984), little is known about their physical properties and how these properties vary among behaviors and under different tree substrate conditions. Furthermore, nothing is known about possible sound or vibration receptors. Here we summarize the current knowledge of acoustic communication in bark beetles and hope to advance our understanding of the potential role of vibrations in bark beetle systems.

21.2 Sound Production and Structures

Air- and substrate-borne vibrations produced via stridulation are known to occur in most bark beetle genera, and vibrational signals are proposed to play important roles in their life history (Barr 1969; Ryker 1988; Lyal and King 1996; Kerchev 2015). Like most coleopterans, sounds are delivered via stridulation, which involves the use of two structures, the 'plectrum' or the 'scraper' that is moved across a ridged surface commonly known as the 'file' or 'pars stridens' (Wessel 2006; Rosado-Neto and dos Santos 2010). Additionally, it is possible that some beetle species rub or scrape their exoskeleton against substrates to evoke vibrations (Drosopoulos and Claridge 2006). Within the bark beetle subfamily Scolytinae, there are five known stridulatory mechanisms. These include the (1) gular-prosternal, where the pars striden is located ventrally on the head and is scraped against the plectrum, consisting of a single or multi-ridged structure at the anterior end of the prosternum; (2) elytral-abdominal (Fig. 21.2), where the pars stridens located on the ventral side of the elytra (usually more prominent on one elytron) is scraped by the plectrum (sclerotized peg) located on the seventh segment of the abdominal tergite. A slightly different elytral-abdominal mechanism is proposed for some female *Dendroctonus* beetles in that an elytral file, similar to that found in males, is located on the sutural margin of the right elytra and a sternal plectrum is located on the inside wall of the last sternite (Rudinsky and Michael 1973); (3) vertex-pronotal (Fig. 21.3), where the pars striden, an elongate, ridged structure present on the vertex of the head, is scraped against the plectrum, a multi-ridged structure present at the ventral anterior side of the pronotum (Barr 1969); (4) abdominal, where a sclerotized peg present on the eighth abdominal segment is scraped against a pars stridens on the posterior region of the last sternite (Rudinsky and Michael 1973); and (5) elytral-tibial, where the pars stridens on the outer margin of the elytra, starting at the level of the boundary between abdominal sternites III and IV, is rubbed by the plectrum, which is a large acicular spine on the inner surface of the hind tibiae (Sasakawa and Yoshiyasu 1983; Kerchev 2015). Each of these mechanisms produces somewhat distinct acoustic patterns and frequency components. One factor that can affect acoustic frequency is body size, but only if the mechanism relates

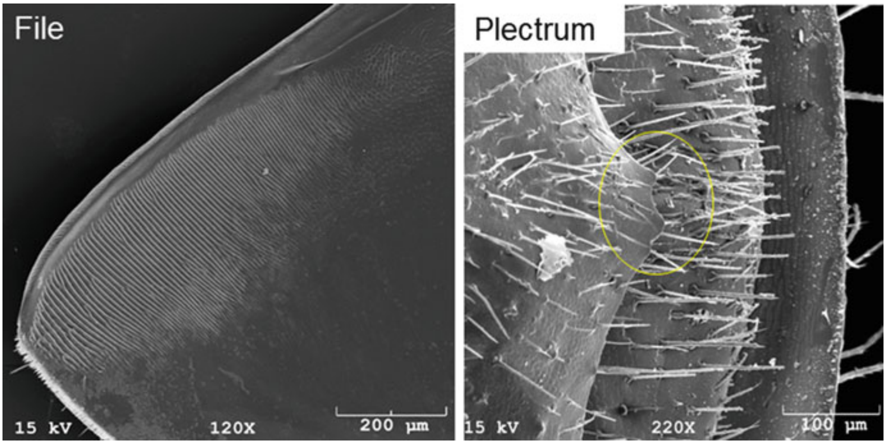

Fig. 21.2 File (underside of elytra) and plectrum of *Dendroctonus approximatus*. Picture by K. Yturralde, Scanning Electron Image, Northern Arizona University

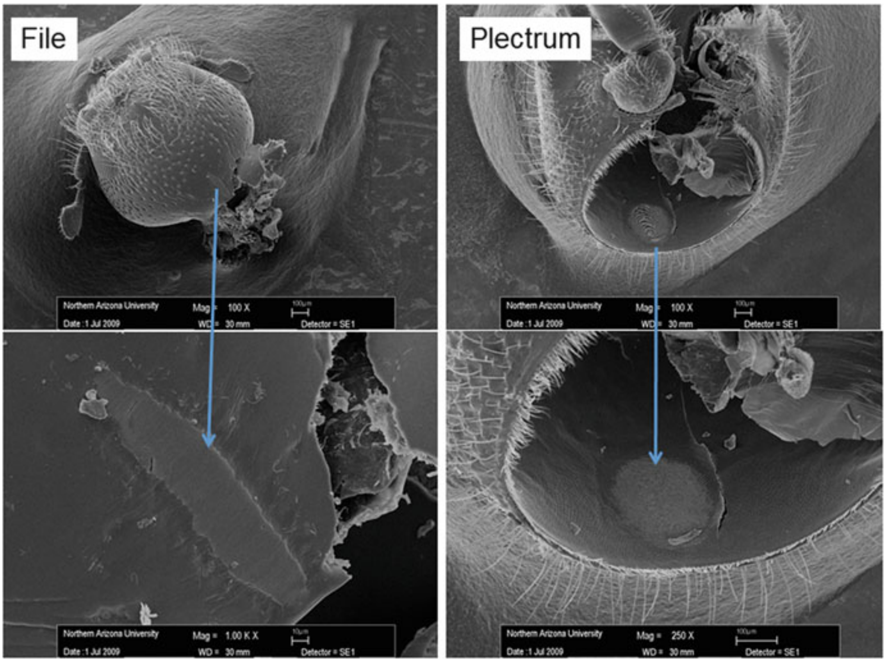

Fig. 21.3 File (anterior dorsal head) and plectrum (dorsal underside of pronotum) of *Ips pini*. Picture by K. Yturralde, Scanning Electron Image, Northern Arizona University

proportionally to body size, or if body cavity size directly influences frequency (Yturralde 2013; Lindeman 2016). Studies have shown that beetles using the elytral-abdominal stridulation method (e.g., *Dendroctonus* beetles) have an inverse correlation between body size and frequency, but other stridulatory methods such as the vertex-pronotal stridulation method (e.g., *Ips* beetles) are not correlated with frequency.

The extent to which beetles stridulate and the physical mechanism employed often differs between the sexes within a species, depending on which sex initiates the construction of the nuptial gallery (Barr 1969). For instance, the vertex-pronotal mechanism (Fig. 21.3) is generally found in non-host selecting females of polygamous species in the genus *Ips* and *Gnathotrichus* (Wilkinson 1962; Wilkinson et al. 1967; Barr 1969; Swaby and Rudinsky 1976). The elytral-abdominal type of stridulatory mechanism (Fig. 21.2) is observed in non-host selecting males of monogamous species in the genus *Dendroctonus*, *Hylesinus* and *Polygraphus* (Vernoff and Rudinsky 1980; Ryker 1988; Kerchev 2015). While the gular-prosternal mechanism can be observed in both sexes of some monogamous (e.g., *Scolytus* spp.) and polygamous (e.g., some *Ips* spp.) species (Barr 1969). In some species, one of the sexes may have two stridulatory mechanisms, such as *Dryocoetes autographus* females, which have the elytral-abdominal and vertex-pronotal stridulatory mechanism (Sasakawa and Yoshiyasu 1983), or *Cryphalus* *fulvus* males, which use the elytral-abdominal mechanism during aggression with other males, but use the vertex-pronotal mechanism during male-female interactions (Sasakawa and Sasakawa 1981).

The mechanics of sound production have only been described for a few bark beetle species. Lindeman (2016) determined that chirp production (both simple and interrupted) in *Dendroctonus* beetles was produced by elastic potential energy, like a stretched spring. Potential energy is stored as the plectrum locks onto the file and remains stationary while the abdomen moves posteriorly, resulting in an increased angle between the plectrum and abdomen (Lindeman 2016). Thus for the elytral-abdominal stridulation mechanism, sound is produced during the down stroke of the plectrum against the pars stridens. Sound that occurs on the upstroke is termed ‘trailing chirps’, which are infrequent but may occur (Lindeman 2016). For intermediate calls, the intervals between phrases occur from a stop in movement in the down stroke of the plectrum against the elytra. This was further confirmed by Lindeman (2016), who determined that the number of teeth on the pars stridens match closely the number of pulses (strikes). A similar elastic mechanism works for species that use the gular-prosternal or vertex-pronotal stridulation mechanisms. As the head prepares to move backward or forward, potential energy is stored as the plectrum begins to push against the pars stridens.

21.3 Sound Perception by Bark Beetles

Given that beetles stridulate and produce a variety of purported call types (see Sect. 21.4), it can be hypothesized that beetles have receptor organs (see Figs. 21.4, 21.5, 21.6). However, no receptor organs have been located in bark beetles. Surprisingly, receptor organs have only been described in a few Coleoptera species. For example, a Johnston’s organ has been described in whirligig beetles (Gyrinidae) (Kolmes 1983; Bendele 1986) and tympanal hearing organs in tiger beetles (Cicindelidae) and scarab beetles (Dynastinae) (Yager and Spangler 1995). In beetles with tympana, the hearing organs act mainly as sense organs for recognizing the ultrasonic sounds from predatory bats (Forrest et al. 1997). Like many other species living within wood and trees (e.g., termites, social wasps, bees, and ants), or living on surfaces similar to the phloem (plant stems; e.g., leaf hoppers), bark beetles likely possess sensitive vibration detectors. More insects use the vibratory channel than use airborne sound for communication (Michelsen et al. 1982; Virant-Doberlet and Čokl 2004; Yack 2016).

Bark beetle stridulation sounds are broadband, exceeding 85 kHz in some recordings (Yturralde 2013; Fleming et al. 2013). The high sonic and ultrasonic frequencies of bark beetle signals provoke questions about a hearing mechanism capable of perceiving these signals. However, the range at which beetles hear is not known. Here we present results of a playback study, where male *D. adjunctus* beetles were placed in phloem sandwiches (Aflitto and Hofstetter 2014) and subjected to artificially generated calls of different frequencies and call durations. Playback calls

Fig. 21.4 Blue arrows point to potential hearing organs on the wings and abdomen of *Ips pini* and *Dendroctonus adjunctus*. Pictures by R. Hofstetter, Northern Arizona University

ranged in band frequencies of 1–100 Hz, 100–5000 Hz, 5000–10,000 Hz, 10,000–25,000 Hz, and 25,000–40,000 Hz and durations of 1, 10, 40, 160, and 640 ms. We found that beetles would call back only to sounds in the band frequencies of 100–5000, 5000–10,000, and 10,000–25,000 Hz and durations of 10, 40, or 160 ms. Although this is not a perfect test of what beetles can hear, it does give some insight into the call characteristics that beetles may be responsive to or are capable of hearing. There is a clear need for more advanced research into the functions, characteristics and receptor mechanisms of the acoustic communication in bark beetles, and beetles in general.

Fig. 21.5 Interior of pronotum with head removed of *Dendroctonus adjunctus*. Arrows point to potential sound receptor organs within the body. Picture by R. Hofstetter, Northern Arizona University

21.4 Acoustic Ecology and Use by Bark Beetles

Given that bark beetles communicate in small galleries within trees, beetles might be hypothesized to communicate by near-field airborne sounds and solid-borne vibrations. Bark beetle stridulations typically produce sounds that are broadband, with multiple peak frequencies ranging from 1 to 80 kHz (Fleming et al. 2013; Lindeman and Yack 2015). Many species are reported to signal in more than one behavioral context, and sounds are often assumed to be used during species recognition, premating interactions, pair formation, mate selection, intraspecies aggression, territoriality and predator deterrence (Barr 1969; Rudinsky 1969; Rudinsky and Michael 1972; Rudinsky et al. 1973; Rudinsky and Ryker 1976; Ryker and Rudinsky 1976a, b; Yandell 1984; Ryker 1988; Lindeman and Yack 2015). Bark beetles typically produce three call forms: single clicks, simple chirps or interrupted chirps. Single clicks are usually produced by the sex that has less pronounced stridulatory structures (e.g., female *Dendroctonus* or male *Ips*) and the stridulation mechanism is poorly understood. Clicks usually occur as a single pulse, but multiple consecutive pulses can be produced. Unlike clicks, chirps contain many pulses (i.e., tooth strikes). Both interrupted and simple (uninterrupted) chirp forms

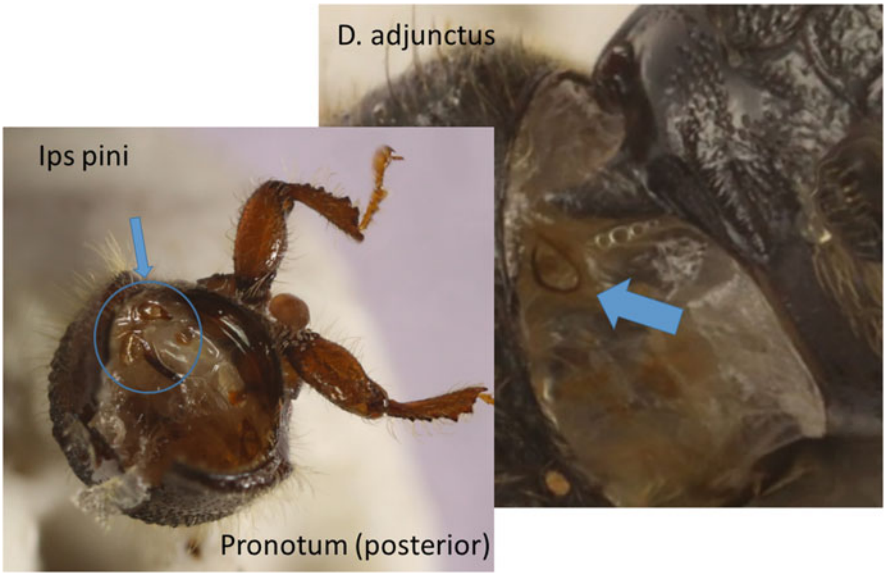

Fig. 21.6 Posterior of pronotum of *Dendroctonus adjunctus* and *Ips pini* (with abdomen removed). Blue arrows (and circle) point to spiracles, which may serve as sound receptor organs. Picture by R. Hofstetter, Northern Arizona University

(Fig. 21.7) may occur within wave trains; however, in some genera, interrupted chirps may be rare (as in *Ips pini*; Dobai et al. 2018).

Simple chirps are significantly shorter than interrupted chirps (Fig. 21.7), with chirps containing one set of tooth strikes and interrupted chirps containing two to five sets of strikes within a phrase (e.g., Michael and Rudinsky 1972). Lindeman and Yack (2015) quantitatively defined chirp type produced based on the minimum inter-tooth strike interval that could be considered a "gap" to classify chirps as interrupted. They found that simple chirps contained inter-tooth strike intervals less than 5 ms, while the interrupted chirps also comprised inter-tooth strike intervals less than 5 ms, but more than one quarter (~28%) were greater than 5 ms. Both chirp types can have a similar number of tooth strikes, although interrupted chirps tend to include more strikes (Fleming et al. 2013). The interrupted chirps typically have significantly lower mean tooth strike rates and higher mean inter-tooth strike intervals (Fleming et al. 2013). Within a beetle species, simple chirps usually have lower dominant peak frequencies than interrupted chirps (Yturralde and Hofstetter 2015; Fleming et al. 2013).

Whether simple or interrupted chirps vary between contexts is poorly understood for most species (Fleming et al. 2013; Lindeman and Yack 2015; Yturralde and Hofstetter 2015). Past studies refer to the chirp types as "attraction," "premating," "rivalry," or "distress" chirps (Barr 1969; Ryker and Rudinsky 1976b; Oester et al. 1978; Ryker 1988; Michael and Rudinsky 1972); however, chirp characteristics may differ between contexts and require verification for many species. Understanding

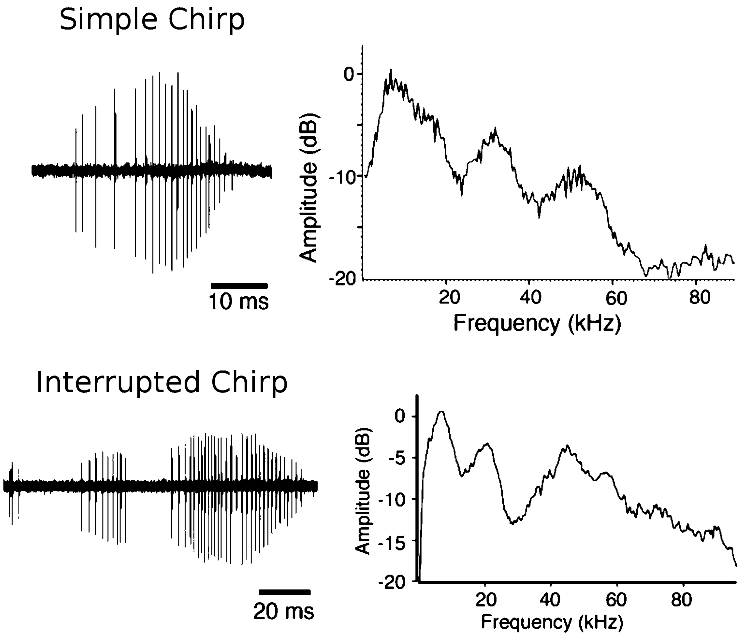

Fig. 21.7 Simple and interrupted chirps showing individual tooth strikes and power spectrum for each chirp type of *Dendroctonus ponderosae*. Adopted from Fleming et al. 2013. © 2008 Canadian Science Publishing or its licensors. Reproduced with permission

how signals vary between contexts can be further complicated in the literature, as signals were recorded under artificial settings that may not represent natural conditions (Wilkinson et al. 1967; Swaby and Rudinsky 1976; Yturralde and Hofstetter 2015). Additionally, beetles appear to produce a variety of calls during encounters or under different situations. Several authors have found that beetle individuals produced both simple and interrupted chirps, but vary in the ratio of interrupted to simple chirps under a variety of situations (Fleming et al. 2013; Lindeman and Yack 2015; Yturralde and Hofstetter 2015). Beetle condition or body size may also influence the ratios of simple and interrupted chirps produced or the characteristics of the chirps (e.g., larger male *Dendroctonus valens* tended to produce interrupted chirps with more components; Lindeman and Yack 2015).

Acoustic signals appear to mediate pheromone production in many of the aggressive tree-killing bark beetles (Rudinsky and Michael 1972; Pitman and Vité 1974; Ryker and Rudinsky 1976a, b; Pureswaran et al. 2016; Liu et al. 2017). Acoustic communication indirectly functions in moderating aggregation by inducing the release of anti-aggregation or masking pheromones in *Dendroctonus* species (Rudinsky 1969). Males stridulate at the entry hole and induce females to release anti-aggregation pheromones. This consequently results in the loss of attraction by males to the gallery (Rudinsky 1969). Males stridulate in response to pheromones released by virgin females, and females respond by altering (i.e., reducing attractiveness) their pheromone composition (Liu et al. 2017).

It is unclear whether acoustic signals are used to distinguish sympatric bark beetle species. Several studies indicate that acoustic signals may not contain enough information on species identity. In a laboratory cross-mating study, Lewis and Cane (1990) found that the acoustic signals of four closely related *Ips* species, although unique in their characteristics, were not effective in preventing *forced* heterospecific pairings. This suggests that acoustic signals may not serve in species recognition. Alternatively, Pureswaran et al. (2016) found evidence that sympatric *Dendroctonus* species produce acoustic chirps that differ and could potentially be used for mate location and differentiation by males. For example, chirps of *D. brevicomis* females (Fig. 21.8) are longer, more frequent and contained more tooth strikes than those of *D. frontalis* (Fig. 21.8). They also found that males could distinguish between conspecific and heterospecific females when given the choice of pairs of females within tree material. Acoustic call characteristics could be used by males to decide whether or not to enter a gallery. Once inside the female's gallery, a male may use information from female acoustic signals (or other male signals) to decide whether to remain in the gallery. Differences in female chirp parameters may therefore be reinforced by selection (Pureswaran et al. 2016).

Chirp characteristics and type (e.g., simple or interrupted chirps) appear to play a role in mate acceptance. For instance, male *D. valens* that produce interrupted chirps have greater success of entry into female galleries (Lindeman and Yack 2015). In each of the trials where males performed exclusively simple chirps, including those where the male was eventually accepted, females actively resisted entry of the male (Lindeman and Yack 2015). Sivalinghem (2011) found that only *Ips* females that produced acoustic signals were admitted into the gallery (by the male). With *Hylastes* spp., the number of interrupted chirps increases, while the simple chirps decline prior to mating (Sapkota 2017). Lindeman and Yack (2015) suggest that for *Dendroctonus*, a male's acoustic performance may provide the female with information on his vigor, and that gaps in interrupted chirps are produced by a more complex motor performance than required for simple chirps. This more challenging action may be a reliable indicator of fitness (Byers et al. 2010). In any case, premating signals likely provide information about the physical attributes of the signaler, whether it be female (e.g., *Ips*) or male (e.g., *Dendroctonus*) (Byers et al. 2010; Lindeman and Yack 2015).

Female signals may function to mediate spacing and territoriality between conspecifics. In most bark beetle species, galleries rarely collide with each other, and in some cases, galleries nearing collision show a sudden change in direction (Rudinsky and Michael 1973; Byers 1989, 2007; Davis and Hofstetter 2009). It is possible that tunneling beetles produce vibrations, either from stridulation or friction via chewing transmitted through phloem substrate, that announce their presence to neighboring beetles. Such sound vibrations may only be transmitted within 1 cm of the gallery but this is an effective distance to deter traversing and touching of galleries. Additionally, larvae could use chewing sounds to space themselves while tunneling, thus reducing potential competition or harm to each other. Rudinsky and Michael (1973) showed that the distance of nearby conspecific adult females affects female stridulation patterns. *Dendroctonus brevicomis* females emitted significantly

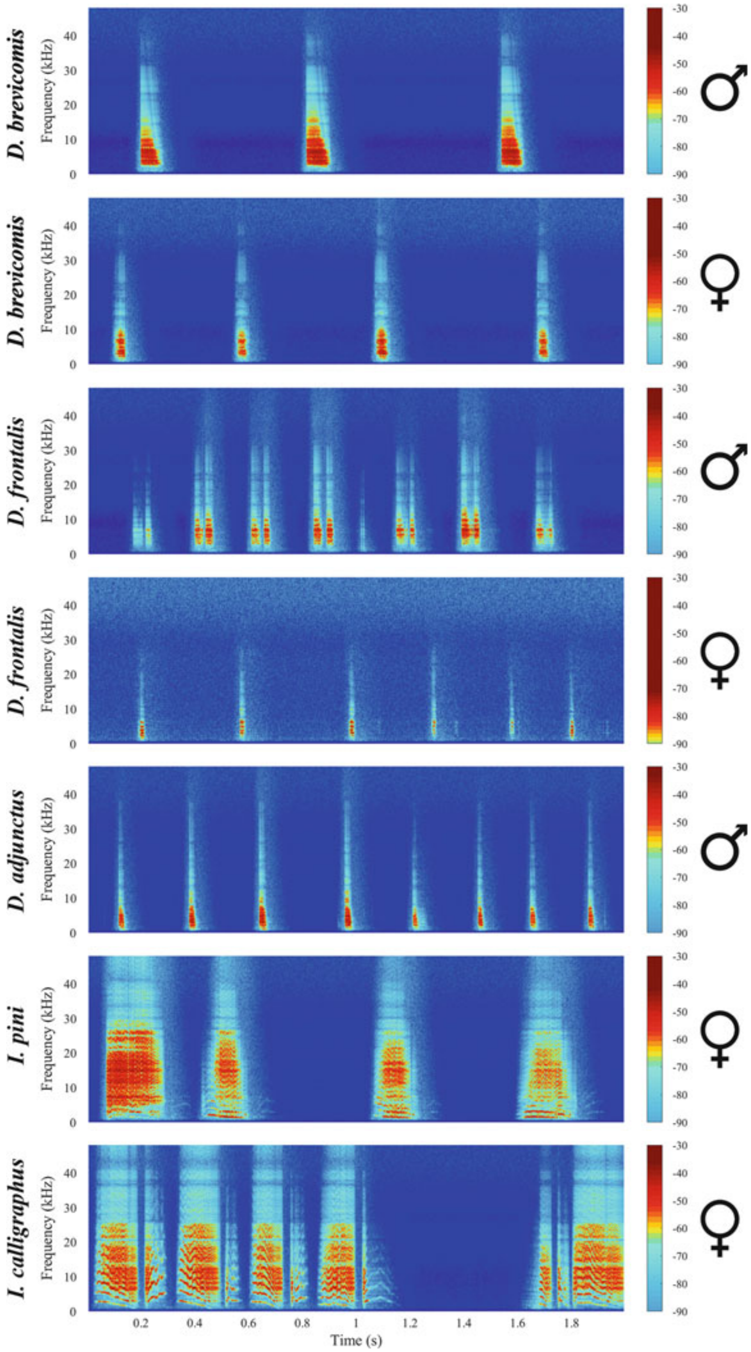

Fig. 21.8 Spectrograms of stridulatory sounds produced by three *Dendroctonus* and two *Ips* species. Color bars in dB. *Dendroctonus* species generate stridulations using an elytro-abdominal stridulatory mechanism; *Ips* species (last two spectrograms), possess a vertex-pronotal organ. No stridulatory sounds have been found in *D. adjunctus* females, and *I. pini* and *I. calligraphus* males. Recordings by C. Bedoya of beetles collected in Flagstaff AZ, USA

more chirps when (two) conspecific females were within 10 cm compared to the number of chirps emitted by solitary females. *Dendroctonus pseudotsugae* females were slightly less sensitive to nearby conspecific females (Rudinsky 1969). Interestingly, neither species changed their vibrational signals when in the presence of heterospecific females at distances of 1–5 cm.

Male-male aggression is common in some bark beetle genera, and males will often produce intense stridulatory vibrations in the presence of other males within their gallery (Rudinsky and Michael 1974; Pureswaran et al. 2016). Studies of *Dendroctonus frontalis* show that males emit a chain of chirps (with a combination of simple and interrupted types) when placed with other males or in response to males entering an already male-occupied gallery. These chirps (sometimes called rivalry chirps) are accompanied by aggressive behavior by both males. A resident male will respond to an intruding male with intense chirping, biting and pushing. When males are confined together in a gallery, long chirp trains occur and intense pushing and biting ensues (Pureswaran et al. 2016). Once out of the gallery, the resident male may continue to chirp and push the other male. Similar behavior has been observed for many *Dendroctonus* species (Rudinsky and Michael 1974) and also between sympatric species of *Dendroctonus* (Pureswaran et al. 2016).

It is unclear whether natural enemies use bark beetle stridulations to locate their prey. Woodpeckers are common predators of many bark beetle species (Schenk and Benjamin 1969; Wegensteiner et al. 2015), and Ramp (1965) showed that the auditory range of the hairy woodpecker had an upper limit reaching 18.5 kHz, which overlaps the frequency of many bark beetle signals (Fig. 21.8). However, attraction of predators to specific beetle stridulations has not been tested. Lewis and Cane (1990) and Sivalinghem (2011) tested whether stridulation by bark beetles would deter or reduce predation events. Lewis and Cane (1990) showed that signaling *Ips calligraphus* females were dropped significantly more often than non-signaling males by a natural beetle predator, *Thanasimus dubius*. Alternatively, Sivalinghem (2011) demonstrated that acoustic signals during predation events were not effective in causing predators to release prey, and the results do not support the "startling function" hypothesis proposed by Lewis and Cane (1990). It is possible that the difference between the studies was due to the differences in beetle size (Lewis and Cane 1990 studied a larger *Ips* beetles), the relatively low sample size in the studies, or that the data may not have been independent as each predator was used more than once in the Lewis and Cane (1990) study. Frazier et al. (1981) investigating predator-prey interactions between *Dendroctonus frontalis* and *T. dubius* found that handling time was significantly higher for male *D. frontalis* than for females. Since male *D. frontalis* produce chirps, sound production may have been a key variable contributing to the longer handling time of males versus females.

Emerging bark beetle progeny or over-wintering adult beetles may use stridulation or other substrate vibrations to coordinate emergence from host trees. No formal studies have looked at the cues or behaviors associated with beetle emergence on trees. Recordings (R.W. Hofstetter, pers. comm.) in the field of overwintering *Ips* and emerging *D. valens* progeny show that beetles may stridulate within the bark prior to emergence.

Mattson and Haack (1987) hypothesized that bark beetles may locate weakened or drought-stressed trees by exploiting the ultrasonic acoustic emissions released by cavitation (Haack et al. 1988). Several studies have shown that when trees experience long periods of dehydration, the water columns in the xylem tissues cavitate, releasing ultrasonic sounds with dominant frequencies ranging from 60 to 300 kHz (Tyree and Dixon 1983; Pena and Grace 1986; Tyree and Sperry 1989). Mattson and Haack (1987) hypothesized that bark- and wood-boring insects could exploit these acoustic cues during host-plant localization. The ultrasonic frequencies of bark beetle signals (Fig. 21.8) implies that bark beetles may be capable of hearing these frequencies, which indirectly supports Mattson and Haack's (1987) hypothesis. Kaiser (2014) tested whether beetles preferred host material that emitted (synthetic) cavitation sounds. He found a greater number of pioneering female *D. ponderosae* chose host material that had high acoustic emissions (produced by ultrasound tactile speakers) versus host material that did not emit ultrasonic sounds. The ability of beetles to identify water-stressed hosts via acoustic cues may be critical to their success at low population densities.

21.5 Vibrations and Movement Within Tree Materials

Many insects use solid-borne vibrations to communicate (Markl 1983; Cocroft et al. 2014; Yack 2016). Bark beetles are capable of producing solid-borne vibrations, but few studies address this specific mode of communication (Fleming et al. 2013; Lindeman 2016). Beetles likely produce two types of vibrations, passive cues produced during chewing of wood or movement within tunnels and active signals produced via stridulation, which were previously referred to as chirps. Vibrations from non-signaling behavior are likely received by predators such as woodpeckers and predatory beetles, as well as neighboring bark beetles and competitors. Sound produced by stridulation, or through friction with the substrate (e.g., mandible-substrate stridulation), by bark beetles conveys messages and is typically stereotyped and conspicuous (Fleming et al. 2013). In most situations with vibrations in wood, the type of vibrations used for communication is almost exclusively restricted to Rayleigh waves (combined longitudinal and transverse waves) or bending waves (Hill 2008). Identifying the type of vibration would provide information on how a given signal would be transmitted (Hill 2008).

We know little about the transmission properties of the phloem in living, dying or dead trees. The phloem's transmission properties are influenced by wood density, deterioration by bacterial, fungal or other boring agents, and moisture content. Phloem and xylem characteristics affect frequencies differently through filtering or by attenuation (Hebets et al. 2008). Bark beetle acoustic behavior and signal properties are likely adapted to accommodate the sound properties of phloem. For example, the broad-band spectra of bark beetle calls may restrict communication to a close range (e.g., Čokl et al. 2004). Close range communication could be an advantage to reduce eavesdropping by predators, limit unintended signals from conspecifics in non-neighboring galleries, and provide a convenient mechanism for limiting overlapping galleries.

Fleming et al. (2013) observed that higher frequency signals (e.g., interrupted chirps during male-male interactions) could be detected by a laser vibrometer several centimeters away from the beetle, but lower amplitude signals were not detected by a laser at distances of 1 cm. Of those chirps that were detected at 1 cm, the vibrations were low amplitude, with a velocity of ~2.7 mm/s. Fleming et al. (2013) notes that the poor signal quality of substrate-borne vibrations compared with airborne sounds could be due to attenuation through the wood but could also be attributable to recording method (i.e., using a laser). Studies (Fleming et al. 2013; Lindeman 2016) show that both air- and substrate-borne vibrations are available to conspecifics at the distances they would normally be interacting, and these close signals could be detected using tympanal ears, near-field sound detectors (e.g., Johnston's organs), or vibration receptors (e.g., subgenual organs) (reviewed in Yack 2004).

We conducted an experiment to evaluate the attenuation effects of the phloem tissue on bark beetle calls (Fig. 21.9). The experiment consisted of recording the sounds produced by individual *Hylastes ater* inside a freshly cut *Pinus radiata* log. To achieve this, an accelerometer was located on the phloem layer of the log at nonlinearly spaced distances from the sound source. Figure 21.9 shows the averaged power spectral densities and energies obtained from five *H. ater* individuals. With distance, the energy decays nonlinearly and the bandwidth shrinks toward the spectral centroid. The phloem tissue acts as a low-pass filter, thus, audible and ultrasonic components above 15 kHz are heavily attenuated regardless of the distance.

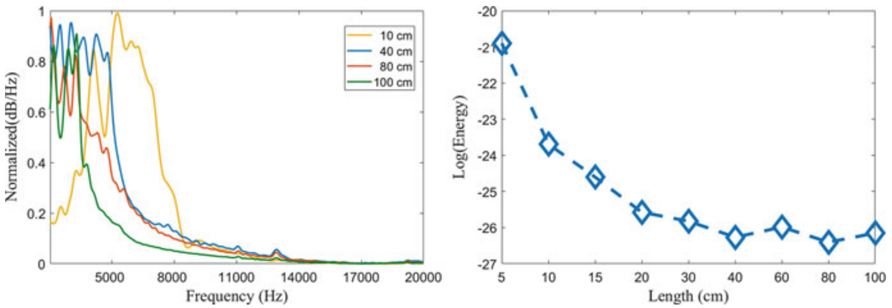

Fig. 21.9 Normalized power spectral density (left) and energy estimated from recordings (right) of *H. ater* calls collected at several distances (10, 40, 80, 100 cm) using an accelerometer located on the phloem tissue of a *P. radiata* log

21.6 Acoustic Technology and Potential Applied Applications

With the exception of olfaction (Borden 1989), the sensory system of bark beetles, along with many other insects, has yet to be leveraged as a management tool. Since bark beetles are more reliant on air- and substrate-borne sounds inside of trees, a place where other sensory modalities are restricted, the application of acoustic-based treatments has the potential to modify behavior in this insulated environment. While the use of vibrations has been largely limited to the detection of wood-infesting insects (Mankin and Moore 2010; Mankin et al. 2011), a few studies have illustrated the efficacy of acoustic treatments that alter behavior.

In one of these studies, Hofstetter et al. (2013) tested the effects of acoustic signals on the tunneling and oviposition of *D. frontalis.* Two sound treatments were administered to a phloem sandwich assay (see Aflitto and Hofstetter 2014): modified *Dendroctonus* beetle calls and an FM radio station. Daily tunneling length was the same in the control (no sound) and radio treatments, averaging 2.1 cm per day. This is contrasted by the modified beetle treatment, which reduced daily tunneling to 0.4 cm per day. The beetle sound treatment also had a strong negative effect on oviposition and only one egg was laid in 15 replicates over seven days compared to 204 eggs from 13 control replicates and 117 eggs from ten radio treatment replicates. Reducing the amount beetles tunnel and oviposit is an important part of the life cycle to target since tunneling contributes to the failure of the tree's vascular system (Bridges et al. 1985; Franceschi et al. 2005).

Automatic acoustic detection and identification of bark beetles is another relevant and understudied area with potential applications (Mankin and Moore 2010; Mankin et al. 2011). Acoustic approaches could be used to study bark beetles without disrupting their natural environment, or to detect them in cases where conventional detection procedures (e.g., visual inspection) are impractical. Additionally, acoustic features could be used as a rapid method of species identification. The wide variety of shapes, sizes, and stridulatory organs makes the call of each bark beetle species unique (Fig. 21.8), and ultimately, a potential taxonomic character. Nonetheless, there is very limited research activity in automatic acoustic bark beetle detection and identification (Lindeman 2016), and no works have addressed the use of these types of methods in the previously mentioned contexts.

Targeting host selection behavior is another aspect of the bark beetle life history where acoustic treatments may be applied. Aflitto et al. (2014) tested whether beetle entry into logs could be affected by acoustic treatments. A choice test assay was used to observe the response of three bark beetle species to four sound treatments: conspecific stress and attraction calls (interrupted calls), longhorn beetle stress call and abiotic tones. The sound treatments affected bark beetle species differently, but the greatest response was found with *D. frontalis* to their stress call, where entry into logs was reduced by 72%. An interesting part of *Dendroctonus* beetle host selection behavior is the use of multimodal communication. For example, *D. pseudotsugae* females colonize a host and quickly begin releasing aggregation pheromones to attract males. Once she identifies a mate via his attraction call, she begins releasing anti-aggregation pheromones to reduce competition for her offspring (Rudinsky et al. 1976). There is potential to hasten the release of these repellent semiochemicals by sonically treating trees with the attraction sounds of male beetles. More research is needed to understand the mechanisms behind how beetles receive acoustic cues and how played-back sounds travel through tree material before it can be used.

There are several challenges to overcome before acoustic treatments are deployed. The current research has tested treatment effects only on portions of trees (e.g., logs, phloem sandwiches). Applying the technology to entire trees will require more testing and inevitably additional modifications. Further, the application of acoustic treatments for stand or landscape-scale outbreaks pose additional challenges such as an efficient way to administer treatments and powering audio devices.

The variety of acoustic tests that have been performed, both under controlled laboratory conditions and in the field, have strongly suggested the efficacy of using sound to affect bark beetle (and other invertebrate) behavior. This research has led to successfully securing patent on a combination of acoustic technologies and associated protocols to disrupt and deter wood-infesting insects in trees and wood products (Hofstetter et al. 2010, Patent No.: US 9480, 248 B2). As an applied technology, the device and protocols are flexible enough to encompass a wide range of insects and other invertebrates but has so far been primarily applied to research upon members of the Scolytinae and Platypodinae tribes (Coleoptera: Curculionidae).

The patent describes the use of biologically relevant sounds derived from the normal signals produced by the insects themselves, modified biologically relevant sounds, synthetically produced complex sounds, and various combinations of all of these acoustic sources, played back into the acoustic substrates occupied by the target organisms (Hofstetter et al. 2013). The working hypothesis is that exposure to the biologically relevant sounds solicits perceptual attention and "neural" readiness that is forced to constantly shift in an unpredictable and exhausting manner since the sounds are presented as a random and quickly shifting playback. Responses to the playback of biologically relevant sounds can be both predictable and dramatic.

Synthetic sounds are generated from a novel network of electronic circuits based upon the mathematics of deterministic chaos (Hofstetter et al. 2013). These circuits produce constantly changing and non-repetitive complex sounds that have very large frequency and amplitude dynamics resulting from a hyper-chaotic state that is autonomous in its behavior. Once set in motion, the circuit network continues to produce novel sounds that appear to be highly disruptive to the target insects since they pass through so many constantly changing auditory behaviors (Hofstetter et al. 2010). Some of these sounds are reminiscent of the insects' own sounds, those of competitive species and potential predatory threats, others that are simply outside of their experiential domain but highly intrusive, and others that appear to mask the normal acoustic communication of the insects themselves. The most important feature of these circuits and their sounds is that they make habituation to the simultaneous presentation of all of the treatment sounds unlikely.

Further development of the patent toward a commercial prototype is ongoing. This research has been directed toward several areas of potential application. These objectives include the effect of sound at reducing bark beetle attacks and colonization on healthy trees, the effects of these sounds on bark beetle behavior within tree tissues, and the potential use of acoustic methods to reduce beetle reproduction and overall populations. Current work is being dedicated to coding both the playback of biologically relevant sounds and the chaotic circuit network into digital form appropriate for implementation as inexpensive and small digital devices that can be used for the protection and treatment of high-value individual trees, orchards and other agricultural contexts, and wood products. Deployment at the scale of large forests remains impractical at this time.

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