These studies suggest that with further development the acoustical method might provide a quick and easy way of detecting and perhaps even estimating insect populations in stored grain. In our laboratory studies, the probability of detection and accuracy of estimation with an acoustical method appear to be quite similar to those for other methods.

END NOTE

Mention of a commercial or proprietary product in this paper does not constitute endorsement by the USDA.

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ACOUSTIC STUDIES OF DENDROCTONUS BARK BEETLES

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ABSTRACT

The utility of recording, monitoring, and manipulating acoustic signals of destructive bark beetles and some methods of bioassay and analysis related to pheromone research are discussed. J. A. Rudinsky and his research group at Oregon State University utilized particular chirps of males and females to acoustically stimulate pheromone release, for bioassay of odor as possible pheromones, and as indicators of the behavior of beetles hidden under the bark. A summary of the acoustic signals of five species of Dendroctonus, D. pseudotsugae, D. ponderosae, D. brevicomis, D. valens, and D. frontalis, is presented.

RESUMEN

Se discuten la utilidad de grabar, chequear, y manipular las señales acústicas de escarabajos destructores de corteza y algunos métodos de bio-ensayos y análisis re-
In keeping with the purpose of this agroacoustic symposium, this paper considers the practical results obtained from the study of insect acoustics by J. A. Rudinsky and his co-workers at Oregon State University. It describes some of the laboratory methods developed to study destructive bark beetles and brings together and reviews the acoustic signals of five species of *Dendroctonus*. The signaling repertoire of several of these beetles has been obscured until now by non-uniform illustration and by being scattered piecemeal through several papers as different types of signals, i.e., stress, attractant, rivalry, territorial, and courtship signals, were described.

Virtually every important timber species of conifer in North America, excluding redwood and sequoia, are attacked by bark beetles, Family Scolytidae (Stark 1982). The economic impact of one species, the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, was $1.5 million for the states of Oregon and Washington in a non-epidemic year, 1980; and the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, was responsible for over $13 million of losses of pines the same year (Rudelman 1980). Four epidemics of the Douglas-fir beetle between 1950 and 1969 killed 7.4 billion boardfeet of prime timber valued at over $3 billion (Furniss & Orr 1970). Losses of timber in the southern U.S. due to the depredations of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, reach similar proportions (Bronson 1986). Attempts to control infestations of bark beetles are made difficult because the insects are inaccessible except during a brief flight period, spending their lives under the bark of trees (Rudinsky 1962). Therefore, research focused upon pheromones as a possible means of control (Rudinsky 1963).

Stridulation by species of *Dendroctonus* was mentioned as early as 1909 (Hopkins 1909), and chirping was identified by Chapman (1955) as a characteristic of males. Allen et al. (1958) published oscillograms of a pair of *D. pseudotsugae* beetles chirping beneath the bark of a Douglas-fir tree. The elytro-abdominal stridulatory apparatus and method of sound production of several species of *Dendroctonus* was described and illustrated by scanning electron micrographs by Michael & Rudinsky (1972). Wilkinson et al. (1967) reported that females of *Ips calligraphus* (German) attracted to nuptial chambers chirp to polygynous males guarding the entry. Barr (1969) demonstrated similar behavior for *Ips paraconfusus* (LeConte). She proposed that the gender that invades the host is silent, and the gender that is attracted to the invader has well developed stridulation in sound producing species. Males of polygynous species colonize the trees, and females chirp at the entry; conversely, females of monogynous beetles, such as species of *Dendroctonus*, colonize and males chirp. Barr also described three different types of stridulatory organs occurring on numerous species of bark beetles.

Alexander et al. (1963) reported loud chirps coming from the burrow of a skin beetle, *Trox suberosus* Fabricius, and generalized that the chirps of most beetles would likely be of low intensity, close range sounds. The long range signals of beetles, analogous to the songs employed by crickets and other Orthoptera, were expected to be pheromones, chemical signals (Ryker 1975). With this expectation, the idea of studying acoustic signals of economically impacting species of bark beetles seemed unreasoning. However, the chemical communication system of the Douglas-fir beetle, our number one
target insect at Oregon State University in the 1970's, was so complex and difficult to analyze that it became apparent that an understanding of the acoustic signals might be useful in manipulating the beetle's signaling behavior for pheromone analysis (Rudinsky & Michael 1972).

Rudinsky (1968) made a discovery that underlined the importance of acoustic signals for understanding the behavior of the Douglas-fir beetle. He had attracted thousands of flying beetles to caged logs infested with female Douglas-fir beetles. After he placed a male with each female in her burrow (gallery), the attractiveness of the logs was completely extinguished within minutes. The effect was so dramatic that Rudinsky hypothesized the release of an antiaggregation pheromone, which he called "the mask." Further, he found that the male did not have to enter the female's burrow for the pheromone mask to be produced, but it did have to be able to chirp. Surgically silenced males had no effect, but normal males that chirped continually while on the screen over the entry triggered the masking effect (Rudinsky 1968, 1969, Rudinsky & Ryker 1977).

Acoustic signals still are not considered promising as population control tools, but they became invaluable for analysis of the various pheromone components. Indeed, the communication system of Dendroctonus bark beetles cannot be understood or explained without detailed knowledge of the acoustic signals. Acoustic signals were of value: 1) as stimuli to cause males or females to release pheromones for analysis; 2) as indicator responses of beetles during behavioral bioassays of possible chemical stimuli; 3) as indicators of the timing of release of pheromones during natural interaction between the male and female; 4) as indicators of passive vs aggressive behavior during natural beetle interactions; and 5) as releasing signals in the chain of stimuli and responses that allow destructive bark beetles to select host trees, to attack en masse, and to regulate the density of the attack, preventing overcrowding and subsequent starvation (Rudinsky 1968, Rudinsky & Ryker 1977, Alcock 1981, Ryker 1984). These studies have resulted in the patenting of methylcyclohexenone as a control pheromone for the Douglas-fir beetle (Rudinsky 1974) and the identification of endo-brevicomin and verbenone as antiaggregation pheromones with potential as control substances for the mountain pine beetle (Ryker & Yandell 1983, Borden et al. 1987).

SOUND RECORDING METHODS

Test beetles were obtained each spring by cutting sections of logs from infested trees, holding them in the warmth of a greenhouse while the brood matured, and then storing the infested logs in walk-in coolers at 4°C until needed. All species of Dendroctonus can be sexed by the presence of a sclerotized pectrum on the seventh abdominal tergite only in males (Michael & Rudinsky 1972). Females were introduced into holes drilled into the bark of freshly cut logs and given 36 h to begin a burrow and produce attractive frass (bark shreds and fecal pellets containing tree odors and pheromones). At this point, a Hewlett-Packard 15119A condenser microphone was placed directly above the entry, leaving space for the tiny male to walk beneath it and enter the burrow (Fig. 1). The signal was amplified by a Princeton Applied Research 113 low noise preamplifier, and recorded on a Nagra 4.2L tape recorder at 38 cm/sec tape speed. Recording system components all showed an essentially flat response from about 0.02 to 22 kHz, and frequencies below 0.3 kHz were filtered by the preamplifier settings to minimize stray noise. Signals were monitored via earphones and an oscilloscope, and signal parameters were measured on a Tektronix 5103N storage oscilloscope. Stored tracings were photographed by a Polaroid® camera (Rudinsky & Ryker 1976).

ACOUSTIC STIMULATION METHOD FOR PHEROMONE RELEASE

Pheromone odors were trapped on Porapak Q for gas chromatographic/mass spec-
trometric analysis easily by placing together a male and female Douglae-fir beetle in a short, paper-lined glass vial and trapping odors from purified air flowing over 30 to 50 such vials within a larger glass container. The male would chirp and jostle the female, and they would each release pheromones. Two males confined in a single vial would chirp and fight, and would also release pheromones. However, females would not release their pheromones if placed together. To trigger pheromone release by single females, Rudinsky stimulated them with recorded male attractant chirps played back through a piezoelectric ceramic disk. The disk was pressed to a silicone rubber gasket over an opening in the glass chamber facing the screened ends of the vials, where it acted as a transducer for recorded chirps (Rudinsky et al. 1973, Ryker et al. 1979) (Fig. 2). Only the chirp of males near the females' burrow successfully triggered females to release their pheromones (Rudinsky et al. 1973).
Method for Bioassay of Odors via Chirping Response

Jantz & Rudinsky (1965) tested the responses of male beetles walking on screening above a tiny vial containing either natural attractive frass or a dilute solution of synthesized chemical odors. Their technique was developed further to include monitoring of the presence or absence of chirping (Rudinsky & Michael 1972), and finally the identification of the type of chirp elicited (Rudinsky & Ryker 1976) (Fig. 3). This technique was very helpful in determining when the beetles switched from being attracted to being repelled as the concentration of certain pheromones increased. For example, the pheromone methylocyclohexenone at only 0.002% concentration in a solution of several other attractants (evaporating at about 1 μg/ml) stimulated walking males to double their turning and digging behavior above the test vial, and to double their tendency to emit attractant chirps. Increasing the concentration (and evaporation rate) of methylocyclohexenone 100 times stimulated the male beetles to pass by the vial without stopping and to give aggressive (rivalry) chirps. Flying beetles showed a similar inhibition to attractive traps and logs in the forest in the presence of higher concentrations of this pheromone (Rudinsky & Ryker 1976, 1980). The chirping response of male beetles was similarly used to bioassay candidate odors and concentrations of synthesized pheromones with other species of Dendroctonus (Michael & Rudinsky 1972, Rudinsky & Ryker 1977, Rudinsky et al. 1974, Ryker & Yandell 1983).

Acoustic Signale of Dendroctonus Bark Beetles

The Douglas-fir beetle, D. pseudotsugae Hopkins, emits five known types of sounds (Fig. 4). Females click intermittently in their burrows in the bark. Clicks appear to be
Monitoring Equipment

amplifier

microphone

tape recorder

earphones

oscilloscope

WALKWAY

Fig. 3. Olfactory walkway for testing of various concentrations of candidate pheromones, modified for acoustic monitoring (Rudinsky & Ryker 1977).

territorial signals because other females turn away from established, clicking females as they select a place to cut an entry hole. When she is disturbed by digging or scratching sounds, a female increases the frequency of clicking (Rudinsky & Michael 1973). Thus she clicks when the male digs into the entry, causing him to release concentrated methylcyclohexenone as an antiaggregation pheromone (Rudinsky et al. 1976).

The male attractant chirp is produced by males responding to the pheromones in female frass at the burrow entry (Rudinsky & Michael 1972). A dilute solution of synthesized tree terpenes and pheromones, with methylcyclohexenone in trace amounts, duplicates the effect of frass (Rudinsky 1973, Rudinsky & Michael 1972, Rudinsky & Ryker 1976). This male chirp also signals the female to actively release additional pheromone, including concentrated methylcyclohexenone (Rudinsky et al. 1973), and to stridulate (clicking) loudly (Rudinsky & Michael 1973).

Male Douglas-fir beetles emit an interrupted chirp, the aggressive chirp (= rivalry chirp), when they meet another beetle in a burrow, on which occasion they invariably attack (Fig. 4). Males fight head to head. The female faces away from the male and pushes backward with the heavily armed posterior portion of her elytra, attempting to force the male out of her burrow (Rudinsky & Ryker 1976, Ryker 1984). This is aggres-
Fig. 4. Drawings of oscillograms of stridulations of *Dendroctonus pseudotsugae*, the Douglas-fir beetle. All oscillograms in this paper are to the same time scale; the shortest tracings each have a 0.1 sec. sweep duration.
sive courtship. When unmated beetles or two males meet, both sexes release concentrated methylycyclohexene. This pheromone, even in the absence of another beetle, stimulates males to give the aggressive chirp and to pass by rather than to stop and dig (Rudinsky & Ryker 1976).

The male Douglas-fir beetle courts the female aggressively, with much jostling, biting, and aggressive chirping for about an hour, after which he emits the courtship chirp (Fig. 4). While giving the courtship chirp, the male strokes the female gently. Copulation follows within minutes (Rudinsky & Ryker 1976). Males give the stress chirp when disturbed (Fig. 4) (Rudinsky & Michael 1972).

The mountain pine beetle, *D. ponderosae* Hopkins, males and females each emit two chirps (Fig. 5). Females click intermittently in their burrows in the bark; this is presumed to have a territorial function (Rudinsky & Michael 1973). The female produces a multi-impulse chirp when the entry is disturbed by digging or scratching, and when defending her burrow against intruders, a territorial function. She ceases to chirp only when touched by a chirping male (Ryker & Rudinsky 1976a). If the male beetle does not chirp correctly, the female attacks and repels him from her burrow if possible, chirping continually.

Male mountain pine beetles give the attractant chirp, an interrupted chirp, when stimulated by the odor of female frass or a synthetic pheromone mixture (Michael & Rudinsky 1972, Ryker & Yandell 1983, Yandell 1984). This chirp also accompanies aggressive behavior whenever unmated beetles meet or when rival males fight (Rudinsky et al. 1974). A male also gives this chirp while digging through frass to enter the female's burrow and while attacking his future mate; this aggressive phase of courtship lasts only a few minutes before mating (Ryker & Rudinsky 1976a).

Mountain pine beetle males produce the simple chirp both when disturbed (stress) and during courtship. Within five minutes of contacting the female, the male ceases to attack the female, begins to stroke her, and gives simple chirps. Copulation follows (Ryker & Rudinsky 1976a).

The western pine beetle, *D. brevicomis* LeConte, female has two and the male has three chirps (Fig. 6). Females click intermittently (about 8 clicks per minute) when alone in their burrows. When disturbed by other females boring nearby (Rudinsky & Michael 1973), or when a male enters her burrow, they give a multi-impulse chirp about twice per second.

Males emit an interrupted chirp with two or three subchirps when attracted to female frass (attractant) (Rudinsky & Michael 1974) and when courting the female (Fig. 6).

The male rivalry chirp is an interrupted chirp with an average of about five subchirps (Fig. 6) and is given during fighting (Rudinsky & Michael 1974). Males also emit a simple stress chirp when disturbed.

The red turpentine beetle, *D. valens* LeConte, male has two distinctive chirps and the female emits several rather variable sounds (Fig. 7). Males produce a simple chirp when attracted to female frass; the stress chirp given by the male when disturbed is not measurably different (Ryker & Rudinsky 1976b).

The "agreement" chirp is a grating sound emitted by a female when a male is digging and chirping in her entry. This is possibly a territorial signal. When first contacted by a male, females produce a much shorter and less variable chirp, the "greeting" chirp. Females also produce stress chirps, containing only about five pulses of sound (Fig. 7). This is the only species of *Dendroctonus* known to do so.

The rivalry or aggressive chirp of male beetles is produced during fighting, as well as during the first 30 seconds of courtship. The entire train of sounds is an interrupted chirp, made by a single motion of the abdomen (Ryker & Rudinsky 1976b).
Fig. 5. Drawings of oscillograms of stridulations of *Dendroctonus ponderosae*, the mountain pine beetle.
Fig. 6. Drawings of oscillograms of stridulations of *Dendroctonus brevicomis*, the western pine beetle.
Fig. 7. Drawings of oscillograms of stridulations of *Dendroctonus valens*, the red turpentine beetle.

The southern pine beetle, *D. frontalis* Zimmermann, is diminutive compared to the other species of *Dendroctonus*, but it is a remarkable chirper. Males readily produce many stress chirps when disturbed (Fig. 8). The male attractant chirp is an interrupted chirp produced when the male is digging in the frass of a virgin female (Rudinsky & Michael 1974).
Fig. 8. Drawings of oscillograms of stridulations of *Dendroctonus frontalis*, the southern pine beetle.

A female produces a series of chirps (about eight per second) when a male enters her burrow. Female chirps are probably territorial signals (Rudinsky & Michael 1973).

Males defend their burrows, fighting other males and producing long, fast series of rivalry chirps (Fig. 8). These chirps are high-pitched, brief, and are delivered at a rate of about 16 per second (Rudinsky & Michael 1974, Rudinsky et al. 1974).

**Functions of Acoustic Signals**

All five species of *Dendroctonus* reviewed in this paper show aggressive behavior in both sexes. Colonizing females compete for limited and ephemeral host material, have territorial clicks or chirps, and attack strangers. Males both fight over control of a female's burrow and test the female for fitness by attacking her (Alcock 1981, Rudinsky & Ryker 1976, Ryker 1984). Specific chirps are associated with fighting; these signals either cease or are replaced by a distinctive courtship signal before mating. This suggests that aggressive chirps are important to the reproductive success of male *Dendroctonus*. Excluding *D. ponderosae*, these species of *Dendroctonus* also have a distinctive signal to the female as they locate the entry of her burrow (attractant chirp). This signal has been shown in two species to trigger an interaction between the female and the male that results in release of antiaggregation pheromones (Rudinsky et al. 1976), thus protecting their brood resources from pressure of over-population and warning
flying beetles to seek more sparsely settled trees. Alcock (1981) gives a convincing argument for individual selection vs signal selection for the benefit of the population. Such closely interlocked acoustic and chemical signals are most complex in species of Dendroctonus bark beetles that attack and overwhelm living trees en masse. Similarly complex development of acoustic and chemical signals, especially territorial and aggressive sounds, might be expected in other highly competitive species of bark beetles (Swedenborg et al. in press).

APPENDIX

A list of acoustic studies of bark beetles other than Dendroctonus, arranged by host tree, follows:

On pine: *Ips calligraphus* (Germar), Wilkinson et al. (1967); *Ips paraconfusus* (LeConte), Barr (1969); *Ips pini* (Say), Oester & Rudinsky (1975), Swaby & Rudinsky (1976).

On spruce: *Ips concinnus* (Mannerheim), Oester & Rudinsky (1975, 1979); *Ips plastographus* (LeConte), Oester & Rudinsky (1979); *Ips tridentis* (Mannerheim), Oester and Rudinsky (1975, 1979); *Ips typographus* L, Rudinsky (1979); *Polygraphus rugipennis* Kirby, Rudinsky et al. (1978); *Hylurgops rugipennis* (Mannerheim), Oester et al. (1978).


On apple: *Scolytus mali* Bechst, Rudinsky et al. (1978b).

On elm: *Hylurgopus rugipes* (Eichhoff), Swedenborg et al. (in press).

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