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Title: SOUND PRODUCTION AND STRIDULATORY ORGANS OF DENDROCTONUS_____

PONDEROSAE HOPKINS: A COMPARISON OF POPULATIONS FROM THREE_____

PINE HOSTS_____

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Populations of Dendroctonus ponderosae Hopkins from three pine

hosts, Pinus ponderosa Laws., P. contorta Dougl. and P. monticola

Dougl., were sampled with regard to their acoustic signals, the

morphology of their stridulatory apparatus and some aspects of their

emergence behavior. Comparisons of these characteristics were made

between samples from different hosts and/or years.

Statistical comparisons were made of acoustic signals in four

behavioral contexts: male attractant stridulation, male rivalry

stridulation, male stress stridulation and female acoustic response to

an intruder. Four parameters were considered: the number of spikes

per chirp, the spike rate, the duration of the chirp and the number of

subchirps per chirp. Differences, in both multivariate comparisons of

all stridulation parameters simultaneously and in comparisons of

individual parameters, existed between samples in all behavioral

contexts except male attractant stridulation. On this basis, male

attractant stridulation is ruled out as a possible interpopulation isolating mechanism.

Seven different morphological characters were measured: the length of the left elytron, the length of the elytral pars stridens, the number of ridges in the elytral pars stridens, the percentage of ridges in the posterior half of the elytral pars stridens, the distance between the spines of the male plectral processes, and the length and number of ridges of the female sternal pars stridens. Statistical comparisons of individual characters were made between samples and between males and females of the same sample. Where differences were significant, D. ponderosae from ponderosa pine were always larger than D. ponderosae from western white pine which were in turn always larger than D. ponderosae from lodgepole pine. In samples from all three hosts females were larger than males in the length of the left elytron and in the percentage of ridges in the posterior half of the elytral pars stridens but generally similar in the length and number of ridges in the elytral pars stridens.

Several differences in emergence behavior existed between populations from white pine and populations from either ponderosa or lodgepole pine. White pine samples had a greater proportion of males emerging than ponderosa and lodgepole samples and the proportion of males emerging did not increase over the emergence period in white pine samples as it did in both ponderosa and lodgepole samples. Emergence of beetles from white pine was rhythmic and closely synchronous with temperature whereas emergence from ponderosa and lodgepole tended to be rhythmic but asynchronous with temperature.

SOUND PRODUCTION AND STRIDULATORY ORGANS OF

DENDROCTONUS PONDEROSAE HOPKINS: A COMPARISON

OF POPULATIONS FROM THREE PINE HOSTS

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

SOUND PRODUCTION AND STRIDULATORY ORGANS OF
DENDROCTONUS PONDEROSAE HOPKINS: A COMPARISON
OF POPULATIONS FROM THREE PINE HOSTS

INTRODUCTION

The mountain pine beetle, Dendroctonus ponderosae Hopkins has, in the past several years, been the most destructive (Forest Pest Conditions, 1980) of the twelve species of Dendroctonus bark beetles occurring in western North America. It infests many species of pines throughout western Canada, the western United States and northern Mexico, and has been reported to occur in epidemic numbers "almost continually" (Furniss and Carolin, 1977) in one or more of its principal hosts. Four of these hosts: Pinus contorta Dougl., P. ponderosa Laws., P. lambertiana Dougl. and P. monticola Dougl. are economically and ecologically important in Oregon.

A question of some controversy has been whether mountain pine beetle behavior conforms to the Hopkins' host selection principle. This principle (as applied to bark beetles) states that a beetle emerging from a given host species will tend to select and infest the same species of tree. If this principle is operative for the mountain pine beetle a complex of populations infesting different hosts should occur in nature. The ability of emergent D. ponderosae to infest different hosts is known (Richmond, 1933) and there is some evidence that host switching occurs in nature (Richmond, 1933; Baker et al., 1971) but it is not known if this is a typical or an unusual occurrence. Several recent studies (Stock and Guenther, 1979; Stock

and Amman, 1980; Sturgeon, 1980) have compared different populations
of the mountain pine beetle electrophoretically to look at possible
enzymatic differences among populations. The present study considers
mountain pine beetle populations from three hosts: <u>Pinus</u> <u>ponderosa</u>
(symbolized as "P"), <u>P</u>. <u>contorta</u> (L) and <u>P</u>. <u>monticola</u> (W) and compares
these populations on the basis of their stridulatory behavior, the
morphology of their stridulatory apparatus and several aspects of
their emergence behavior. Differences in the signal parameters
investigated are known to affect pheromone-release behavior in both
sexes of the Douglas-fir beetle (Rudinsky and Michael, 1972; Rudinsky
<u>et</u> <u>al</u>., 1976) and may thus affect reproductive behavior. Female <u>D</u>.
<u>pseudotsugae</u> release an anti-aggregant pheromone in response to a
male's "attractant" stridulation but not to male "stress" stridulation
and male pheromone release is stimulated by female stridulation but
not by male stridulation. It is conceivable that host-related
differences in any of the three categories investigated in the present
study could either be a result of the occurrence of host populations
or could lead to the establishment of host populations by ultimately
resulting in isolating mechanisms. The present study seeks to add to
the knowledge of variation among populations of the mountain pine
beetle from different hosts. The specific objectives were:

1. To describe and compare stridulation of <u>D</u>. <u>ponderosae</u> populations
   in each of four behavioral contexts.

   a. Male attractant stridulation.

   b. Male rivalry stridulation.

  c. Male stress stridulation.

  d. Female response to male intruder stridulation.

2. To describe and compare the stridulatory apparatus of D.
 ponderosae populations considering seven characteristics.

  a. Length of the left elytron.

  b. Length of the pars stridens of the left elytron.

  c. Number of ridges on the pars stridens of the left elytron.

  d. Percentage of ridges in the posterior half of the elytral pars
   stridens.

  e. Distance between the male plectral processes.

  f. Length of the female sternal pars stridens.

  g. Number of ridges on the female sternal pars stridens.

3. To investigate and compare the emergence behavior of D. ponderosae
 considering three aspects.

  a. Sex ratio.

  b. Emergence density.

  c. Temporal emergence pattern.

It has been generally accepted that the process of animal speciation usually occurs among allopatric populations which diverge genetically over extended periods of time (Mayr, 1963). Genetic divergence may occur as a result of the operation of different selective pressures and/or stochastic processes (Brown, 1975). Reproductive isolation between two populations may be a byproduct of such genetic divergence or may be a direct result of selection in cases of secondary contact between populations where hybrids are less fit than either of the parents (Ayala, 1975). Gene flow between populations has been thought to be the cohesive force in the maintenance of species integrity by preventing genetic divergence (Mayr, 1963). Yet, Ehrlich and Raven (1969) cite examples of species that have had little or no gene flow between allopatric populations over many generations and that exhibit little variation. Conversely, animal populations may be effectively separated by short distances (Ehrlich and Raven, 1969), even with considerable gene flow, and sympatric populations may be greatly differentiated as the result of different selective regimes (Endler, 1973; 1977). The effect of gene flow in retarding differentiation among populations, either allopatric or sympatric, may be much less than is commonly believed (Ehrlich and Raven, 1969). Bush (1975) has presented a case for sympatric speciation based on studies of Rhagoletis fruit flies, sibling species developing from host races preferring different food plants.

Mountain pine beetle populations exhibit marked variation in morphology (Lanier and Wood, 1968; Sturgeon, 1980), host preference

(Wood, 1963; Baker et al., 1971), emergence behavior (Billings and Gara, 1975) and in their response to pheromone components (McKnight, 1979). Allopatric and sympatric divergence of D. ponderosae populations are distinct but not exclusive possibilities; both could result, in time, in some sort of isolating mechanism which may function to prevent matings of individuals from different sympatric or alloparapatric populations.

Isolating mechanisms, a frequent though by no means inevitable result of the process of speciation, may arise when different selective regimes act on two populations (Ehrlich and Raven, 1969). Several researchers have proposed that differences in acoustic signals may serve as isolating mechanisms. Walker (1957) documented that females of the tree cricket genus Oecanthus were selectively attracted to songs of males of their own species even against a background of songs from other species. Perdeck (1958) reported that song was the primary isolating mechanism between two sympatric grasshopper species, Chorthippus bruneus Thunb. and C. biguttulus L. Van Tassell (1965) suggested that premating chirps might function as an isolating mechanism for sympatric species of the aquatic genus Berosus (Coleoptera: Hydrophilidae). Four species of the genus Homorocoryphus (Orthoptera: Tettigonoidea) appear to use song as an isolating mechanism, the males of the species repeating a single tone at species specific rates (Bailey and Robinson, 1971). Ryker (1975) proposed that two species of Tropisternus (Coleoptera: Hydrophilidae) are separated reproductively, at least in part, by having distinctive calling chirps.

In the Scolytidae, it has been suggested that stridulation functions in species recognition among three sympatric Ips species (Oester and Rudinsky, 1979). Ryker and Rudinsky (1976) demonstrated that the male "interrupted chirp" functions as a recognition signal for the mountain pine beetle by surgically silencing males which were subsequently rejected by unpaired females. There can be little doubt that different species of pine impose different selective pressures, both physically and physiologically, on infesting beetle populations (Powell, 1967; Sturgeon, 1980). Therefore, if divergent selection is operating, any trait that helps maintain the integrity of populations from specific hosts might be selected for unless there is a greater adaptive advantage in retaining the ability to switch hosts. Divergence in recognition signals that tended to reduce matings between individuals emerging from different species of pine would be a likely result of such selective pressures.

A. D. Hopkins (1909) originally described two species of Dendroctonus, D. ponderosae and D. monticolae, which were commonly called the Black Hills beetle and the mountain pine beetle respectively. Hay (1956) experimentally crossed the two presumed species; the results indicated that they should be considered one species. Wood (1963) revised the genus and synonomized the two, along with D. jeffreyi, under D. ponderosae. Smith (1965) experimented with the response of D. ponderosae (= monticolae) and D. ponderosae (= jeffreyi) to pine resin components and noted physiological differences between the two. Later, Lanier and Wood (1968) reinvestigated the morphology and karyology and cross-mated the three original species.

They concluded that the synonomy of D. ponderosae and D. monticolae should be maintained but that D. jeffreyi should be separated.

Adult mountain pine beetles are stout, cylindrical and black, and range in length from less than 4.0 to 7.5 mm (Hopkins, 1909; Beal, 1939; Amman and Pace, 1976). Adult females mine in the inner bark, scoring both the bark and the wood, and construct egg galleries about 5 mm in width that may extend over 60 cm in length (Evenden et al., 1943). These galleries generally begin with a slight sideways crook near the entrance and then proceed rather directly up the bole of the tree although the galleries may wind irregularly in sugar pine (Evenden et al., 1943). The eggs are small, oval, pearly white and approximately 0.8 mm in diameter and are laid singly in niches cut on both sides of the gallery (Hopkins, 1909). After a few days the larvae hatch from the eggs as white, legless grubs with brown head capsules (Hopkins, 1909). In the process of feeding the larvae produce galleries at right angles to the egg galleries (Evenden et al., 1943). The larvae pass through four stadia (Amman, 1978) and finally form pupal cells between the bark and wood (Beal, 1939). The pupae are white and have visible adult characteristics (Hopkins, 1909). The teneral adults mature over the course of several weeks and may emerge through individual exit holes or may congregate with the result that several beetles emerge through a single exit hole (Evenden et al., 1943). The timing of emergence varies but adults may emerge from sometime in the spring into September in different parts of the beetle's range (Evenden et al., 1943). Reemergence of adult males is common, less so for the females; however, some females may reemerge

and attack as many as three times (DeLeon et al., 1934; Evenden et al., 1943). Throughout much of its range the mountain pine beetle is univoltine but in the southern, warmer areas it may have two and part of a third generations in one year; conversely, at high elevations and in the colder reaches of its range, two years may be required for the development of a single generation (Evenden et al., 1943).

Bark beetles lead a rather cryptic life, spending almost their entire life cycle in or beneath the bark of their host tree (Rudinsky, 1962). The main exception to this is during the flight period when the beetles fly to locate suitable hosts for colonizing or maturation feeding. The dispersal flight of mature mountain pine beetles in the Pacific Northwest occurs most often in late July or early August (Reid, 1962). It is the female mountain pine beetles that select and initiate the attack of host trees. The manner in which initial host selection is accomplished has not yet been clarified. Renwick and Vité (1970) suggested that females are initially attracted to resin components of potential host trees. The response of some other scolytids in flight to host resin volatiles has been previously demonstrated (Rudinsky, 1963; Vité et al., 1964). A second hypothesis proposes that beetles are not, in the strict sense of the word, attracted to potential host trees, but that they land on all trees, host and non-host alike, and that host selection occurs after the females have landed (Wood, 1972). Hynum and Berryman (1980) reported that mountain pine beetles land randomly with respect to tree volatiles and dbh in lodgepole stands, though they tend to remain on

the largest lodgepole in a stand (Cole and Amman, 1969; Roe and Amman, 1970).

After selecting a host tree, female mountain pine beetles construct a gallery. In the process of feeding and defecating they release several compounds which are either tree- or beetle-produced (Pitman et al., 1968; 1969; Rudinsky et al., 1974). trans-Verbenol, a beetle-produced compound, serves as a population aggregating pheromone (Pitman et al., 1968) when synergized by tree-produced terpenes such as α-pinene or myrcene (Pitman, 1971). This pheromone attracts beetles of both sexes to the tree. Rudinsky et al. (1974) suggested that exo-brevicomin (Pitman et al., 1969) and endo-brevicomin inhibit the attractive properties of trans-verbenol and α-pinene in ponderosa pine stands. In recent studies in both lodgepole and ponderosa pine stands in central Oregon it has·been demonstrated that racemic exo- and endo-brevicomin (Ryker and Rudinsky, 1982) and racemic frontalin (Ryker and Libbey, 1982) all inhibit the response of flying D. ponderosae to an attractant mixture of trans-verbenol and terpenes. McKnight (1979) noted differences in the responses of populations from different hosts to stereoisomers of α-pinene and trans-verbenol as well as to exo-brevicomin and suggested that the differences were due to the divergence of these populations with respect to their chemical communication systems. Complicating the chemical communication is the interplay of beetle acoustic signals. Chemoacoustic interaction has been demonstrated for other Dendroctonus species (Rudinsky, 1968; Michael and Rudinsky, 1972; Rudinsky and Michael, 1973; Rudinsky et al., 1973; Rudinsky and Ryker, 1976) and has been shown to occur in

D. ponderosae; males have been stimulated to emit "attractant chirps"
when exposed to the odor of female frass (Michael and Rudinsky, 1972).

The uses of sounds by arthropods for communication are well
documented (Haskell, 1961; Busnel, 1963; Alexander, 1967). The
rubbing together of two specialized body parts is one of the most
common of the several sound-production methods employed by the
Arthropoda. This process is called stridulation (DuMortier, 1963).

Among the Coleoptera, stridulation is common in many groups
(Gahan, 1900) though often it is known in only a minority of species
in any one group, thus supporting the idea of the polyphyletic origins
of sound production in this taxon (Arrow, 1942). Indeed, three
different types of stridulatory organs are found in different species
of a single genus, Ips, in the Scolytidae (Barr, 1969). Among those
beetles known to stridulate are members of the Passalidae (Alexander
et al., 1963), Dytiscidae, Erotylidae and Endomychidae (Arrow, 1924),
Nitidulidae, Tenebrionidae and Chrysomelidae (DuMortier, 1963),
Cerambycidae (Michelson, 1966), Hydrophilidae (vanTassell, 1965;
Ryker, 1975), and Scolytidae (Barr, 1969; Michael and Rudinsky, 1972;
Rudinsky and Michael, 1973; Ryker and Rudinsky, 1976). Alexander et
al. (1963) suggested that there are three stages in the evolution of
stridulation in beetles: the presence of one signal used in only a
single functional context such as a disturbance or stress chirp, one
signal that is used in two separate functional contexts as might be
the case with disturbance/recognition chirps, and two or more
different signals used in two or more different contexts. This third
stage of the evolution of stridulation is well exemplified by various

Dendroctonus and Ips bark beetles (Rudinsky and Michael, 1973;
Rudinsky and Ryker, 1976; Swaby and Rudinsky, 1976; Oester and
Rudinsky, 1979).

The stridulatory behavior of the mountain pine beetle has been
previously examined in beetles emerged from ponderosa pine (Michael
and Rudinsky, 1972; Rudinsky and Michael, 1973; Ryker and Rudinsky,
1976). Males were shown to have at least two basic types of
stridulation, "simple" and "interrupted chirps", which were used in
different behavioral situations (Michael and Rudinsky, 1972). The
simple chirp (Figure 1a) was emitted by the males in both hand-held
stress situations and during courtship, that is, when the male had
joined the female in her gallery and had begun nudging and stroking
her during a period immediately preceeding copulation (Ryker and
Rudinsky, 1976). The interrupted chirp (Figure 1b) was observed
during male attraction behavior, when the male sought to enter the
gallery of an attractive female, and during rivalry behavior, as when
two males fought in the gallery of an attractive female (Michael and
Rudinsky, 1972).

Female mountain pine beetles have also been shown to have two
types of stridulation, a click, a single spike of sound produced
occasionally when the female is alone in her gallery (Figure 2a), and
a simple, multi-pulse chirp emitted whenever any beetle disturbed the
entry or entered her gallery (Figure 2b) (Ryker and Rudinsky, 1976).
This multi-pulse chirp has also been heard when other females begin to
bore galleries nearby. It has been suggested that this chirp may

serve a territorial function in spacing beetle attacks in the host tree (Rudinsky and Michael, 1973).

The morphology of the stridulatory apparatus has been previously described for mountain pine beetles emerged from ponderosa pine (Michael and Rudinsky, 1972; Rudinsky and Michael, 1973). Hopkins (1909) described a similar stridulatory apparatus for Dendroctonus valens, and Lyon (1958) described it in several Dendroctonus species. The male plectrum (Figure 3) consists of a pair of spines or processes located medially and posteriorly on the seventh abdominal tergite. Dendroctonus males have an elytral file or pars stridens (sensu DuMortier, 1963) which consists of a tear-drop shaped series of transverse teeth or ridges that occurs most strongly on the medial-ventral portion of the left elytron and continues somewhat weakly on the right elytron such that when the elytra are locked together the two portions compose one continuous file (Michael and Rudinsky, 1972). To stridulate, the male moves its abdomen anteriorly and dorsally so that the plectrum engages the pars stridens. The plectrum is then drawn posteriorly down the file, each ridge or tooth producing a single spike of sound as may be seen in oscillographs of its chirps.

In female Dendroctonus the posterior of the eighth abdominal tergite, called the pygidium, is heavily chitinized and appears to serve as the plectrum (Rudinsky and Michael, 1973). In this function the pygidium may engage either of two pars stridens, the elytral file, located posteriorly along the medial margin of the ventral side of the left elytron, or the sternal file, which is found on the anterior wall

of the last sternite, opposite the pygidium (Rudinsky and Michael, 1972).

Figure 1.   Oscillograms of male D. ponderosae simple chirp (a)
and interrupted chirp (b).
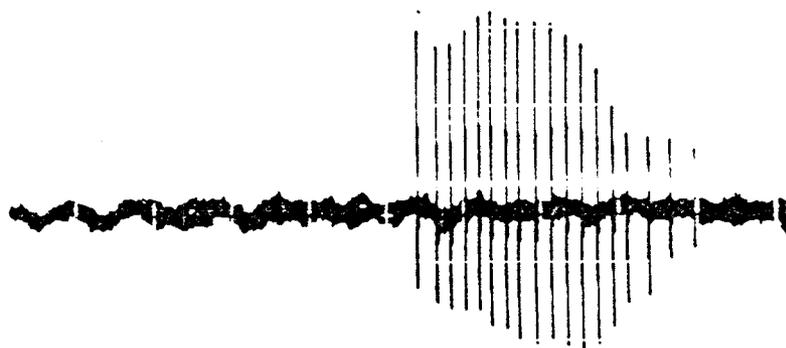
1a.

_____ 18 msec _____
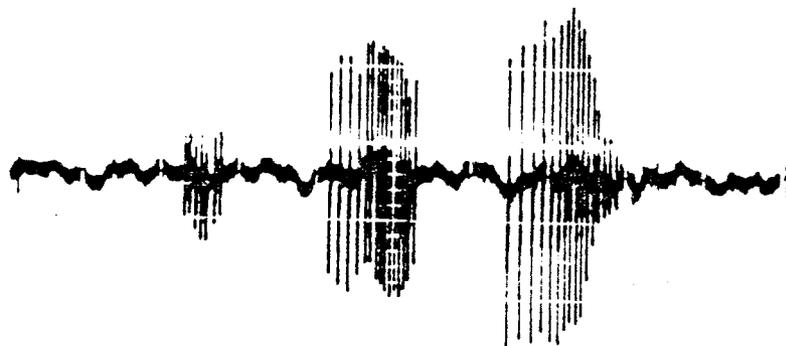
1b.   _____ 180 msec _____

Figure 2. Oscillograms of female D. ponderosae click (a) and
simple chirp (b).
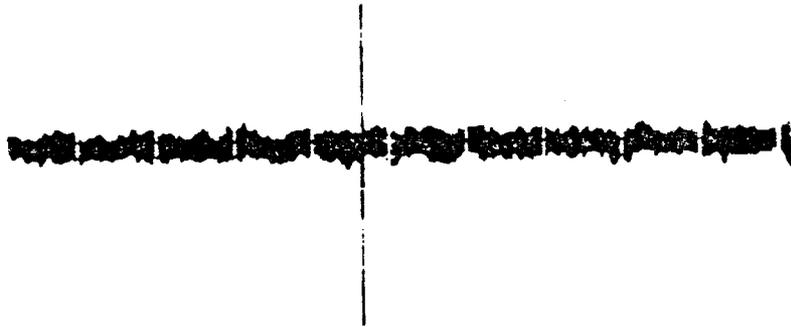
2a.   ___40 msec___
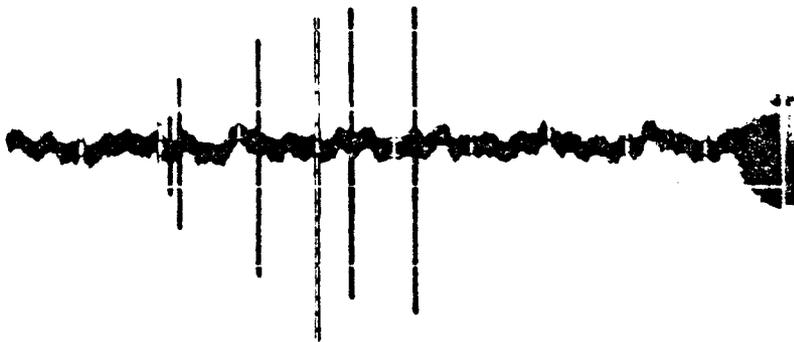
2b.   ___40 msec___

Figure 3. Dorsal view of seventh and eighth abdominal tergites
of male Dendroctonus beetles (a) and plectrum of
male Dendroctonus beetles (b). After Michael and
Rudinsky (1972).

3a.

3b.
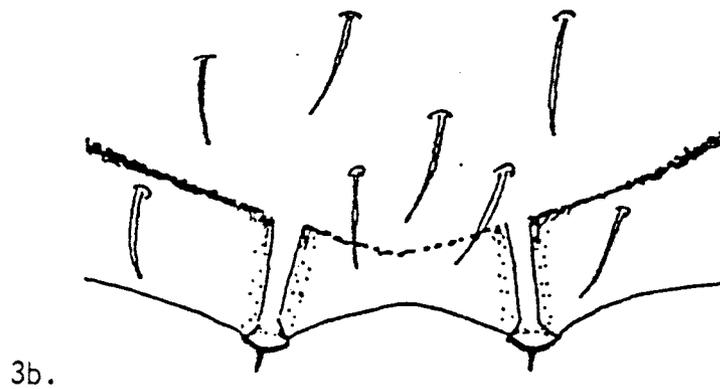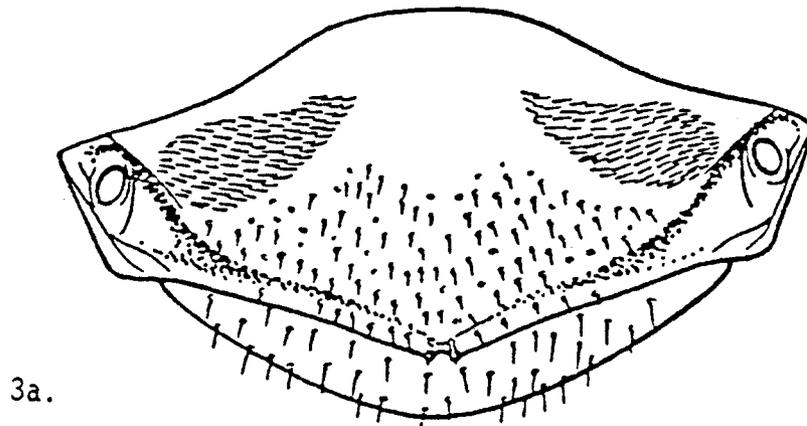
MATERIALS AND METHODS

Trees naturally infested by the mountain pine beetle were felled in the spring before emergence began with the single exception of one white pine (WII) which was cut in the preceeding fall and left in the field through the winter. Three trees were sampled from all sites but one (Table 1) where only a single tree was sampled. In all cases, billets were cut both from the base of the tree and from the uppermost area of infestation. The infested billets were moistened and covered to prevent desiccation, transported to the Forest Insect Lab in Corvallis and placed in the greenhouse where the mountain pine beetle broods completed development.

Acoustic Behavior

For the acoustic studies, beetles were selected at random from beetles emerging during approximately one week when the emergence was at or near its peak. The sound equipment employed has been previously described (Ryker and Rudinsky, 1976) and consisted of a Nagra 4.2L tape recorder, a Princeton Applied Research Model 113 low noise pre-amplifier, and a Hewlett Packard Model 15119A condenser microphone. Beetle stridulation was recorded at a tape speed of 38 cm/sec. The system exhibited a flat response from 0.02 - 22.0 kHz. Signal parameters were measured from sounds displayed on a Tektronix Model 5103N storage oscilloscope. All recordings were made at temperatures of 26 - 28°C between 9:00 a.m. and 4:00 p.m.

To record male attractant stridulation, emergent females were introduced into logs taken from a freshly cut, uninfested tree of the

same species from which they emerged. The females were allowed to feed for one day at approximately 27°C. Males were removed from the refrigerator where they were kept in cold storage at 3 - 4°C for a period not exceeding five days, and allowed to warm and become active. A male was then placed gently on the log containing the feeding females so that, in walking forward, it encountered the pile of frass at the entrance to the gallery of a feeding female. The microphone was lowered directly over the male and attractant stridulation was recorded as it dug in the frass and chirped.

Rivalry chirps were recorded from fighting males. A male was introduced into the gallery of an attractive female. This male, the "resident" male, was allowed to establish itself for a minimum of five minutes. Then, a second male, the "intruder", was added. Concurrently, a surgically silenced male was added to the attractive gallery of a second, unpaired female. When the resident male backed out of the gallery towards the intruder, the silenced male was substituted for the intruder. As the resident and the silenced males fought in the attractive female's gallery or near the entrance, the stridulation of the resident male was recorded. Males were silenced by excising the elytral file, making stridulation impossible, and then leaving them in cold storage for at least 24 hrs at 3 - 4°C (Ryker and Rudinsky, 1976).

Stress chirps were recorded from male beetles while holding them between the thumb and forefinger approximately 0.5 cm below the microphone.

Stridulation of female mountain pine beetles responding to intrusions at their gallery entrances (Rudinsky and Michael, 1973) was recorded. A male was allowed to discover and dig in the gallery entrance of a female established in a freshly cut log for 24 hrs. When the female reacted to the intruding male by chirping, the male was replaced by a second, silenced male. Female stridulation was recorded as the silenced male dug in the frass at the gallery entrance.

In characterizing the stridulation of the mountain pine beetle, terminology consistent with that employed by previous workers in this area has been used (Michael and Rudinsky, 1972: Rudinsky and Michael, 1973; Ryker and Rudinsky, 1976). Chirp is used to denote "the shortest unitary rhythm element of a sound emission that can be readily distinguished as such by the unaided human ear" (Broughton, 1963). As viewed on an oscilloscope, a simple chirp is composed of a series of sound impulses or spikes, each spike produced by a "single toothstrike of the plectrum on the file" (Ryker and Rudinsky, 1976). Simple chirps are produced by a single abdominal movement. An interrupted chirp also is produced by a single movement of the plectrum over the pars stridens but with the series of pulses interrupted by one or more brief periods of silence. Thus, the interrupted chirp, which is emitted only by male mountain pine beetles, consists of two or more sub-chirps with gaps of silence between them.

Sound parameters were measured by displaying the recorded chirps on a storage oscilloscope at a tape speed of 19 cm/sec. The sound parameters measured were the number of toothstrikes per chirp, the

toothstrike rate calculated as toothstrikes per second, the duration

of the chirp and, where appropriate, the number of subchirps per

chirp.

Three groups of comparisons were made in which stridulation in

each of four behavioral contexts (male attractant, male rivalry, male

stress and female response to intruder) was analyzed separately.

1. "Host" Comparisons: In this group all samples from a

    particular host species were combined and comparisons made

    among hosts.

2. L1978 versus LI-III: These comparisons were made because the

    two lodgepole samples were taken from different subspecies of

    Pinus contorta and genetic differences have been shown to

    exist between mountain pine beetle populations from these

    different subspecies (Stock and Guenther, 1979).

3. L1978 versus P1978: These comparisons were made since the

    two samples were taken from geographically proximate

    locations the same year and might best reveal any existing

    host related differences.

In the host comparisons, a T^2 multivariate technique was used

to first compare stridulation between each pair of hosts within each

behavioral context. This technique yielded an F statistic to test the

hypothesis that there was no significant difference between the mean

vectors (of all stridulation parameters) of the samples compared (e.g.

lodgepole versus ponderosa male attractant stridulation with all four

stridulation parameters considered simultaneously). Since each data

set was used in two comparisons a Bonferonni-type multiple comparisons

procedure could be applied. Thus, the type I error for a pair of comparisons could be controlled at 0.05 or 0.01 by using critical values of the test statistic for a single comparison of $\alpha = 0.025$ or 0.005, i.e. $\alpha/2$. Scheffe's significant difference test was employed to look for differences among individual parameters from the three host samples with individual comparisons being conducted at a significance level of $\alpha = 0.0167$ or 0.0033.

In the two groups of comparisons with the L1978 sample, the T^2 multivariate technique was used in comparing all stridulation parameters in a single behavioral context simultaneously. Individual parameters were compared through analysis of variance. A multiple comparison procedure was used with both tests such that the significance level of a single comparison was maintained at $\alpha = 0.025$ or 0.005.

Morphology

Beetles used in the morphological studies were selected at random from all beetles emerging either from a specific tree or from all the trees from a single sample site. Morphological measurements were obtained by surgically removing the structure of interest and mounting it on a microscope slide for examination.

The measurements taken for all beetles sampled were the length of the left elytron (25x magnification), the length of the pars stridens of the left elytron (100x), the number of ridges on the elytral pars stridens (100x), and the percentage of the total number of ridges in the posterior half of the elytral pars stridens (100x). In addition,

the sternal files of the females were measured for length and the number of ridges (430x). Also the distance between the tips of the spines of the male plectral processes was measured (970x) (Figure 3).

Six groups of comparisons were made in which each structure of interest was compared individually between samples.

1. "Host" Comparisons: All samples from a particular host species and sex were combined.

2. Females versus Males: All samples from a particular host were combined.

3. L1978 versus L1979

4. P1978 versus P1979

5. L1978 versus P1978

6. L1979 versus P1979

Comparison 3 considered samples from different subspecies of lodgepole from different years and from geographically separate populations. Comparison 4 considered samples from ponderosa but from different years and separate populations. Comparisons 5 and 6 involved samples taken from different hosts the same year and from sample sites not so greatly separated that the populations weren't potentially inter-breeding.

In the host comparisons, analysis of variance (ANOVA) was used to test for differences among treatment (host) means at $\alpha = 0.05$ or 0.01. Scheffe's significant difference test was employed to look for differences among individual parameters between each three pairs of hosts with single comparisons at $\alpha = 0.0167$ or 0.0033. In group 2,

ANOVA was used to compare individual parameters within each host at $\alpha = 0.05$ or 0.01.

ANOVA was also used in the last four comparisons to test for differences between means of individual parameters. In these comparisons, a multiple comparisons procedure was used such that individual comparisons were maintained at a significance level of $\alpha = 0.025$ or 0.005 and the significance level for a pair of comparisons (e.g. L1978 versus L1979 and L1978 versus P1978) was subsequently 0.05 or 0.01.

Emergence

Emergence studies were conducted by placing the infested billets in screened cages in the greenhouse, with billets of separate samples placed in separate cages. Collections of the emerged beetles were made on an hourly basis between 7:00 a.m. and 7:00 p.m., or as time allowed. All greenhouse windows were kept open throughout the emergence period to allow temperature and humidity to fluctuate under the influence of external weather conditions. A Foxboro hygrothermograph was placed in the emergence cage to monitor temperature and humidity, and barometric pressure readings were obtained from the U.S. Weather Bureau Station on the Oregon State University campus. When collected, the beetles were either placed in small metal cans with moist paper towels and kept in a refrigerator at 3 - 4°C until sexed and used in other studies, or frozen. After the emergence was completed, the billets were measured for length and circumference and the bark surface area was calculated.

Beetles were sexed by the method employed by Lyon (1958), who identified males by the presence of the plectrum on the posterior of the seventh abdominal tergite. In samples P1978, P1979, WI, WII and WIII all of the beetles emerging were sexed. In samples LI-III a total of 682 beetles or 64% of the total emerging were sexed; 621 or 49% of the total number of beetles emerging from LIV-VI were sexed. A minimum of one billet per sample was debarked after the completion of emergence to check for unemerged brood.

The percentages of males in the first 50% and the second 50% of total emergence were compared by ANOVA to look for changes in the sex ratio of emerging beetles over the course of the emergence period. This was done separately for samples from different hosts.

Using data from the emergence of the WI sample, a regression equation was constructed to determine which variables could best be used to predict emergence during a one hour period. The variables considered are listed in Table 2.

Table 1. Samples taken: number of trees, year and location.

Sample symbol	Number of trees sampled	Year	Location
L1978	3	1978	Sec. 16, T. 2 S., R. 36 E. Willamette Meridian. 19.3 km W. of LaGrande, Union Co., OR. 1036 m elevation
LI-III	3	1979	Sec. 9, T. 22 S., R. 12 E., W.M. 3.2 km W. of Paulina Peak, Deschutes Co., OR. 1829 m elevation
LIV-VI	3	1979	Sec. 6, T. 22 S., R. 12 E., W.M. 5.6 km W. of Paulina Peak, Deschutes Co., OR. 1676 m elevation
P1978	3	1978	Sec. 30, T. 4 S., R. 36 E., W.M. 29.0 km S.W. of LaGrande, Union Co., OR. 1967 m elevation
P1979	1	1979	Sec. 7, T. 15 S., R. 12 E., W.M. 6.4 km W. of Paulina Peak, Deschutes Co., OR. 1646 m elevation
WI-III	3	1979	Sec. 20, T. 15 S., R. 7 E., W.M. 11.3 km N.E. of McKenzie Bridge, Lane Co., OR. 975 m elevation

Table 2. Variables used in regression of hourly emergence.

Variable Name	Variable Number	Method of Determination
Emergence	1	Log_{10} (total emergence in 1 hr period + 0.5)
Day	2	Number of days from first emergence
Day squared	3	Variable 2 squared
Day cubed	4	Variable 2 cubed
Hour	5	Time at end of 1 hr period (1-24: 1:00 am - 12:00 midnight)
Hour squared	6	Variable 5 squared
Temperature	7	Average of temperatures at beginning and end of 1 hr period (^{0}C)
Temperature squared	8	Variable 7 squared
Hour/Temperature	9	Variable 5 x variable 7
Humidity	10	Average of relative humidities at beginning and end of 1 hr period (%)
Barometric pressure	11	Average of barometric pressures at beginning and end of 1 hr period (inches of mercury)

RESULTS

Acoustic Behavior

In the host comparisons, the chirping of the males in response to attractive females did not differ significantly (α = 0.025) between males from any two hosts, as indicated by the multivariate T^2 tests (Table 3) (Figure 4). The equivalency of the attractant chirping of beetles from the three host trees was further confirmed in that none of the individual parameters (number of sound pulses per chirp, spike rate, chirp duration and number of subchirps per chirp) differed significantly (α = 0.0167) between beetles from any two hosts. In the comparisons involving the L1978 sample (L1978 vs. P1978 and L1978 vs. LI-III), neither the chirps compared as a whole (α = 0.025) nor the individual parameters differed significantly (α = 0.025) between beetles in either comparison.

In contrast to the male attractant chirping, the comparisons of male rivalry stridulation revealed significant differences between samples. Rivalry stridulation, which consisted of a mixture of simple and interrupted chirps, differed between all samples compared by multivariate analysis at the $\alpha < 0.005$ level with the exception of the L1978 and P1978 samples, which differed at a significance level of $\alpha < 0.025$ (Table 4) (Figure 5). In the host comparisons, the number of spikes per chirp did not differ between beetles of any two hosts (α = 0.05). The spike rate was greater in the ponderosa than in either the white or lodgepole pine samples; the spike rate in the latter two did not differ (α = 0.0167). The duration of the rivalry

chirps was longer and the number of subchirps was greater for the white pine sample than for the ponderosa and lodgepole samples, which did not differ significantly (α = 0.0167) from each other.

The number of spikes, the spike rate and the number of subchirps were all significantly greater in the L1978 sample than in the LI-III sample; the chirp duration did not differ between the two (α = 0.025). In a comparison of the L1978 and the P1978 samples, only the spike rate differed significantly with the pondersa beetles having a higher spike rate than the lodgepole beetles; the other parameters did not differ between these samples (α = 0.025).

Male stress stridulation, like male rivalry stridulation, differed greatly between samples. All T^2 tests for the multivariate comparisons of the mean vectors characterizing male stress chirping were significant at α < 0.005 (Table 5) (Figure 6). The ponderosa beetles emitted more tooth strikes per chirp than the lodgepole beetles and the white pine beetles, and the lodgepole beetles emitted more toothstrikes per chirp than the white pine beetles in the host comparisons. The spike rate was equivalent for the ponderosa and white pine beetles (α = 0.0167) and for the white and lodgepole pine beetles (α = 0.0167) but was greater in the ponderosa sample than in the lodgepole sample. The duration of the stress chirp did not differ significantly (α = 0.0167) between the ponderosa and lodgepole pine samples but was longer in both of these than in the white pine sample.

The comparison of the L1978 and LI-III samples revealed a greater number of spikes and a longer chirp duration in the L1978 sample but a higher spike rate in the LI-III samples. In the L1978 versus P1978

comparison, the number of spikes did not differ significantly (α =
0.025). The spike rate was higher in the P1978 sample and the chirp
duration was longer in the L1978 sample.

A mountain pine beetle female will often respond to a disturbance
at her gallery entrance by backing up towards the gallery entrance
and emitting a series of simple chirps (Ryker and Rudinsky, 1976).
These acoustic responses of females to intruders, like male rivalry
and male stress stridulation, differed between the samples compared.
All multivariate comparisons indicated significant differences between
samples at α = 0.005 (Table 6) (Figure 7). In the host comparisons,
the number of spikes in the female chirp was greater in the white pine
sample than in either the lodgepole or the ponderosa samples, which
did not differ from each other (α = 0.0167). The spike rates of the
white and ponderosa pine samples were not significantly different (α =
0.0167) but were both greater than the spike rate of the lodgepole
sample. The duration of the lodgepole female chirp was greater than
that of either the white pine female or the ponderosa female, which
did not differ from each other (α = 0.0167).

The L1978 and LI-III samples did not differ significantly (α =
0.025) in either the number of spikes per chirp or the duration of the
chirp, differing only in that the spike rate of the LI-III sample was
greater than the spike rate of the L1978 sample. In comparing the
L1978 and the P1978 sample it was found that the number of spikes per
chirp did not differ significantly (α = 0.025). However, the spike
rate and the duration of the chirp did vary significantly, with the

spike rate of P1978 being greater and the chirp duration of L1978

being the greater of the two.

Morphology

Significant differences in male morphology were found in the

"host" comparisons of $\underline{D}$. ponderosae samples from different hosts in

the length of the left elytron (Table 7) (Figure 8), the length of the

pars stridens of the left elytron (Table 8), the number of ridges of

the elytral pars stridens (Table 9) and the distance between the

sclerotized processes of the plectrum (Table 11) (Figure 10). Only in

the comparison of the percentage of ridges in the posterior half of

the pars stridens was no difference found between male beetles of

different hosts (α = 0.05) (Table 10) (Figure 9). The ponderosa and

white pine mountain pine beetle males differed only in that the

ponderosa males had a longer left elytron and a greater distance

between the plectral processes. Male ponderosa beetles had, on the

average, a longer left elytron, a longer elytral pars stridens, more

ridges on the pars stridens and a greater distance between the

plectral processes than did the lodgepole males. The length of the

left elytron, the length of the pars stridens and the number of ridges

on the pars stridens were significantly greater in white pine males

than in lodgepole males. All other host comparisons of individual

characters revealed no significant differences (α = 0.0167) between

samples of males from any two hosts.

Significant differences in morphology between females from

different hosts were found in the length of the left elytron (Table 7)

(Figure 8), the length of the elytral pars stridens (Table 8), the number of ridges on the eltryal pars stridens (Table 9) and the number of ridges on the sternal pars stridens (Table 12) (Figure 11). No differences were found between females of different hosts in the length of the sternal pars stridens (α = 0.05) (Table 12) or in the percentage of ridges in the posterior half of the elytral pars stridens (α = 0.05) (Table 10). As in the males, ponderosa females were, on the average, larger than both the white and lodgepole pine females. The ponderosa females had a longer left elytron, a longer elytral pars stridens and more ridges on the elytral pars stridens than did the white pine females; beetles from the two hosts did not differ (α = 0.0167) in the other three characters measured. The ponderosa females had a significantly longer left elytron, a longer elytral file and more ridges on both the elytral and sternal files than did the lodgepole females. Of the six measured morphological characteristics, the white pine females differed from the lodgepole females only in that they had a significantly longer left elytron. No other significant differences were detected (α = 0.0167) in the host comparisons of morphological characters between female samples of any two hosts.

The comparisons of morphology between the female and male samples from the same host indicated that the females tended to be larger than the males (Table 13) (Figure 8). In comparisons of samples from all three hosts, the females had a significantly longer left elytron than did the males. The females also had a significantly higher percentage of ridges in the posterior half of the elytral file than did the males

from all three hosts. No differences were found between females and males of any host in the length of the elytral file ($\alpha = 0.05$) and only the lodgepole females differed from the males in the number of teeth in the elytral file, with lodgepole females having a greater number. The males from ponderosa and white pine did not differ from the females of the same host in the number of teeth in the elytral file ($\alpha = 0.05$).

Comparisons between samples from the same host species but from different years and locations indicated that, where differences were significant, the sample means from 1978 for both the lodgepole and ponderosa pine beetle samples were larger than the corresponding 1979 sample means. Male L1978 beetles had a longer left elytron, more ridges on the elytral file and a greater distance between the plectral processes than the L1979 males; the other two characters compared did not differ between these samples ($\alpha = 0.025$). Similarly, the P1978 males had a longer elytral file, more teeth on the elytral file and a greater distance between the plectral processes than did the P1979 males although the two samples did not differ in the length of the left elytron or in the percentage of ridges in the posterior half of the file ($\alpha = 0.025$). Sample means for the length of the left elytron in both the L1978 and P1978 female samples were greater than the corresponding sample means from beetles from the same host in 1979. None of the other characters differed between years for female beetles from the same host ($\alpha = 0.025$).

The L1978 versus P1978 and L1979 versus P1979 comparisons gave results similar to the overall "host" comparisons; ponderosa beetles

were larger than lodgepole beetles in both years. P1978 males had a longer left elytron, a longer elytral file and more ridges on the elytral file than the L1978 males. P1979 males had a longer left elytron and a longer elytral file than did the L1979 males. No other characters differed significantly in these comparisons (α = 0.025). The female comparisons yielded similar results. The P1978 females had, on the average, a longer left elytron, a longer elytral file, more ridges on the elytral file and more ridges on the sternal file than the L1978 females; the other characters compared were not significantly different between these two samples (α = 0.025). The only significant difference between sample means in the P1979 versus L1979 female comparison was that the length of the left elytron was longer in the P1979 sample; the other characters compared did not differ significantly (α = 0.025).

Emergence

The overall percentage of males for all beetles that emerged from a particular species of host in the present study varied from 29.9% from ponderosa, to 35.4% from lodgepole and to 47.9% from white pine (Table 14). Beetles emerged in approximately a 1:1 sex ratio from white pine in 1979 and this ratio held true for beetles emerging from white pine taken from the same location the following year but the sex ratio was nearly 1:2 (males:females) for beetles emerging from white pine from the same location in 1981 (unpublished data). Similar year-to-year variation also was observed for mountain pine beetles emerging from sugar pine in 1980 and 1981. The sex ratio was nearly

1:1 in 1980 (331 males to 337 females) but dropped to approximately 1:2 in 1981 (101 males to 211 females) (unpublished data).

During the emergence period, the sex ratio shifted in favor of the males in both lodgepole and ponderosa emergence. No such shift occurred in $\underline{D}$. $\underline{ponderosae}$ emergence from white pine (Tables 15, 16).

Beetle emergence densities in the present study differed greatly between hosts and between samples (Table 14). The lowest average numbers of beetles emerging per m^2 of bark surface were from the P1978 sample, in which an average of 42 beetles emerged, and from the WII subsample, in which 31 beetles emerged per m^2 of bark surface area (1 m^2 = 10.76 ft^2). Combining the samples from each host resulted in emergence density averages of 419 beetles/m^2 in lodgepole, 64 beetles/m^2 in ponderosa and 632 beetles/m^2 in white pine.

Detailed emergence records were taken mainly from four samples: L1978, P1978, WI and WIII. The maximum daily emergence, here defined as the number of beetles emerged in a 24 hour period from 8:00 a.m. to 8:00 a.m. the following day, occurred for these groups on days 5, 13, 12 and 20 of their respective emergence periods. Fifty percent of the total number of beetles emerged by the 11th day of emergence (L1978), day 14 (WI) and day 17 (WIII and P1978). The length of time required for all the beetles to emerge, the emergence period, varied from 41 days (L1978) and 43 days (P1978) to 51 days (WI) and 54 days (WIII).

In the present study of emergence in the greenhouse, maximum hourly emergence of mountain pine beetles from both ponderosa and lodgepole tended to occur before 1:00 p.m. The emergence of $\underline{D}$. $\underline{ponderosae}$ from white pine was more closely synchronous with ambient

temperature in the greenhouse; the maximum hourly emergence tended to occur between 12:00 noon and 6:00 p.m. The maximum daily temperature almost invariably occurred between the hours of 12:00 noon and 6:00 p.m. in the greenhouse during the emergence studies.

In the regression of D. ponderosae emergence from white pine on several independent variables only five variables were found to be important in explaining variation in the emergence variable: day, day squared, day cubed, temperature and temperature squared. Temperature was the single most important variable in predicting hourly emergence. Three regression equations were constructed: one with just the temperature variables, one with only the day variables, and a final equation containing all five independent variables.

1) Emergence = (-)4.072 + 0.35 (Temperature) - 0.0063

(Temperature squared).

The analysis of variance table for this regression (Table 17) indicates that the regression is significant at $\alpha < 0.01$ and that 27.41% of the variation in the dependent variable, emergence, can be accounted for by variation in the independent variables.

2) Emergence = (-)0.13 + 0.18 (Day) - 0.0096 (Day squared)

+ 0.00013 (Day cubed).

The analysis of variance table for this regression (Table 18) indicates that the regression is significant at $\alpha < 0.01$ and that 23.81% of the variation in the dependent variable can be accounted for by variation in the independent variables.

3) Emergence = (-)4.55 + 0.31 (Temperature) - 0.0052

(Temperature squared) + 0.19 (Day) - 0.0098 (Day

squared) + 0.00013 (Day cubed).

The analysis of variance table for this regression (Table 19)

indicates that the regression is significant at $\alpha < 0.01$ and that

55.67% of the variation in the dependent variable can be accounted for

by variation in the independent variables.

The first regression equation predicts that emergence should

commence between 16 and 17°C and that hourly emergence should continue

to increase up to about 28 to 29°C, while the third regression sets

these limits at 15° and 30°C. Hourly emergence should begin to

decrease, other things being equal, at between 28 and 30°C.

The second regression equation predicts that hourly emergence

tends to increase with the day after first emergence until about day

13, at which point hourly emergence should begin to decrease. The

equation further predicts that a second inflexion point in the rate of

hourly emergence should occur on about the 35th day. At that point

the effect of increasing the day variable (and thus day^2 and day^3)

is that increasing hourly emergence is predicted, other things being

equal. The final regression predicts that these inflexion points will

occur on days 13 and 36.

Table 3. Male attractant stridulation: means and standard errors of stridulation parameters and statistical results of comparisons between samples of D. ponderosae from different hosts and/or years.

Sample	Spikes/Chirp (no.)		Spike Rate (no./second)		Envelope Duration (msec)		Subchirps/Chirp (no.)		n[1]
	$\bar{x}$	SE($\bar{x}$)	$\bar{x}$	SE($\bar{x}$)	$\bar{x}$	SE($\bar{x}$)	$\bar{x}$	SE($\bar{x}$)	
P1978	34.8	1.72	425	11.0	138	6.7	3.1	0.12	40
WI-III	34.4	0.83	415	9.4	152	4.3	3.4	0.09	120
L(all)[2]	34.0	0.69	401	6.2	149	3.8	3.2	0.06	160
L1978	33.8	2.08	411	12.8	157	6.7	3.2	0.13	40
LI-III	34.0	0.61	397	7.1	147	4.5	3.2	0.07	120

1) Total number of chirps analyzed· 5 chirps analyzed per beetle (Tables 5-8).
2) Combination of L1978 and LI-III samples (Tables 5-8).

Comparison	Significance Level of Comparison				
	Mult.[1]	Spikes/[2] Chirp	Spike[2] Rate	Envelope[2] Duration	Subchirps/[2] Chirp
P1978 vs. WI-III	NS[3]	NS	NS	NS	NS
P1978 vs. L(all)	NS	NS	NS	NS	NS
WI-III vs L(all)	NS	NS	NS	NS	NS
L1978 vs. LI-III	NS	NS	NS	NS	NS
L1978 vs. P1978	NS	NS	NS	NS	NS

1) Statistical results of multivariate T^2 tests comparing samples for equivalency of mean vectors of all stridulation parameters.

2) Statistical results of comparisons of individual parameters.
3) Samples compared not significantly different (see text for level of significance).

Figure 4. Means (horizontal lines) and 95% confidence intervals (vertical lines) of parameters of male D. ponderosae attractant stridulation. Males emerged from ponderosa (P), western white (W) and lodgepole (L) pine. All samples within a host were combined.

4a. Number of spikes/chirp.

4b. Spike rate.

4c. Envelope duration.

4d. Number of subchirps/chirp.
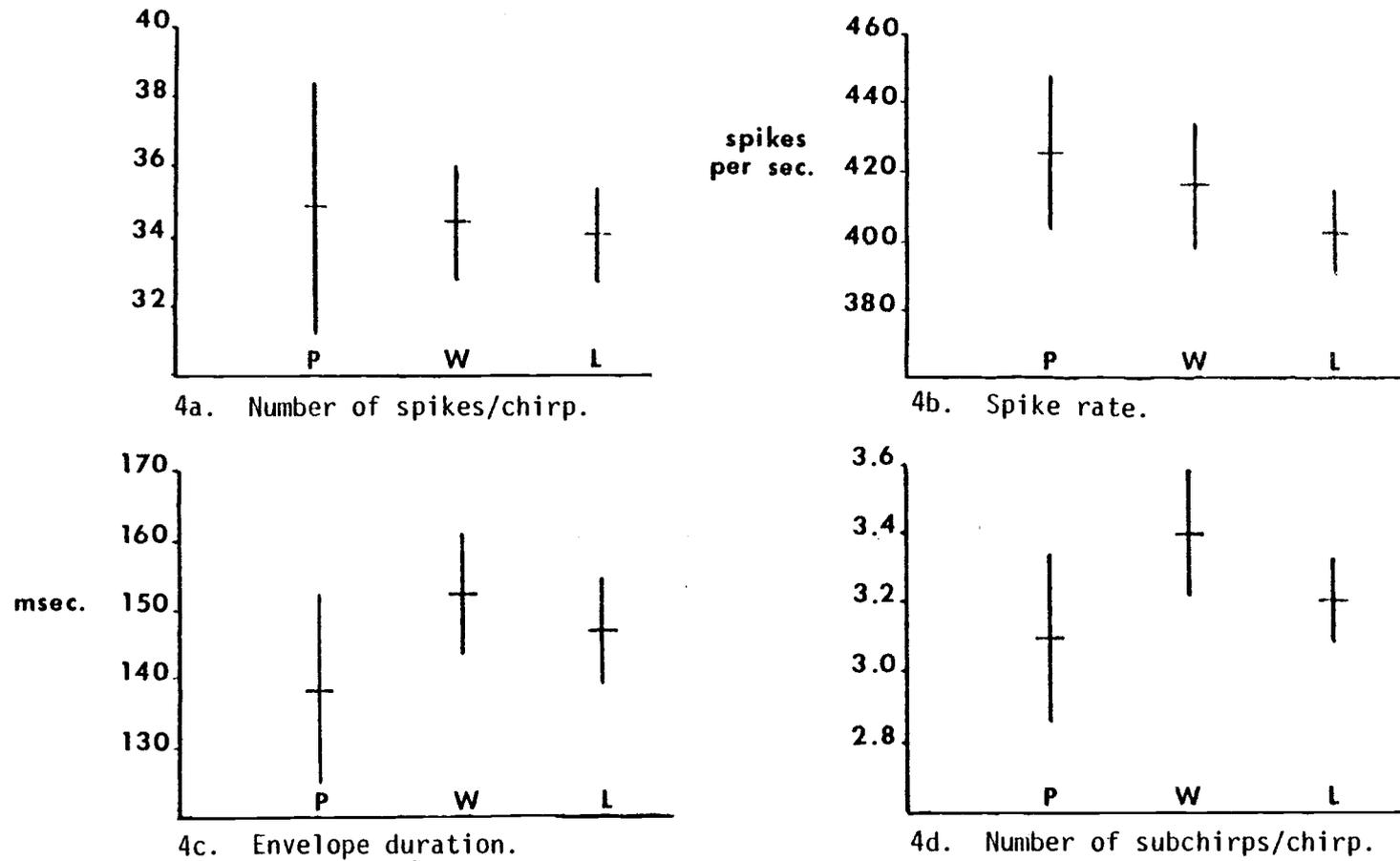
Table 4. Male rivalry stridulation: means and standard errors of stridulation parameters and statistical results of comparisons between samples of $\underline{D}$. _ponderosae_ from different hosts and/or years.

Sample	Spikes/Chirp (no.)		Spike Rate (no./second)		Envelope Duration (msec)		Subchirps/Chirp (no.)		n
	$\bar{x}$	$SE(\bar{x})$	$\bar{x}$	$SE(\bar{x})$	$\bar{x}$	$SE(\bar{x})$	$\bar{x}$	$SE(\bar{x})$	
P1978	28.6	1.18	626	20.4	59	6.4	1.4	0.13	40
WI-III	31.4	1.01	516	24.2	115	9.6	2.6	0.23	40
L(all)	27.6	1.09	476	14.1	71	4.8	1.4	0.10	80
L1978	31.6	1.86	529	19.4	80	8.4	1.6	0.18	40
LI-III	23.6	0.73	423	16.9	62	4.5	1.2	0.07	40

Comparison	Significance Level of Comparison				
	Mult.	Spikes/ Chirp	Spike Rate	Envelope Duration	Subchirps/ Chirp
P1978 vs. WI-III	0.005[1]	NS	0.0033	0.0033	0.0033
P1978 vs. L(all)	0.005	NS	0.0033	NS	NS
WI-III vs. L(all)	0.005	NS	NS	0.0033	0.0033
L1978 vs. LI-III	0.005	0.005	0.005	NS	0.025
L1978 vs. P1978	0.005	NS	0.005	NS	NS

1) Samples compared significantly different at alpha < 0.005.

Figure 5. Means (horizontal lines) and 95% confidence intervals
(vertical lines) of parameters of male D. ponderosae
rivalry stridulation. Males emerged from ponderosa
(P), western white (W) and lodgepole (L) pine. All
samples within a host were combined.

5a. Number of spikes/chirp.

5b. Spike rate.

5c. Envelope duration.

5d. Number of subchirps/chirp.
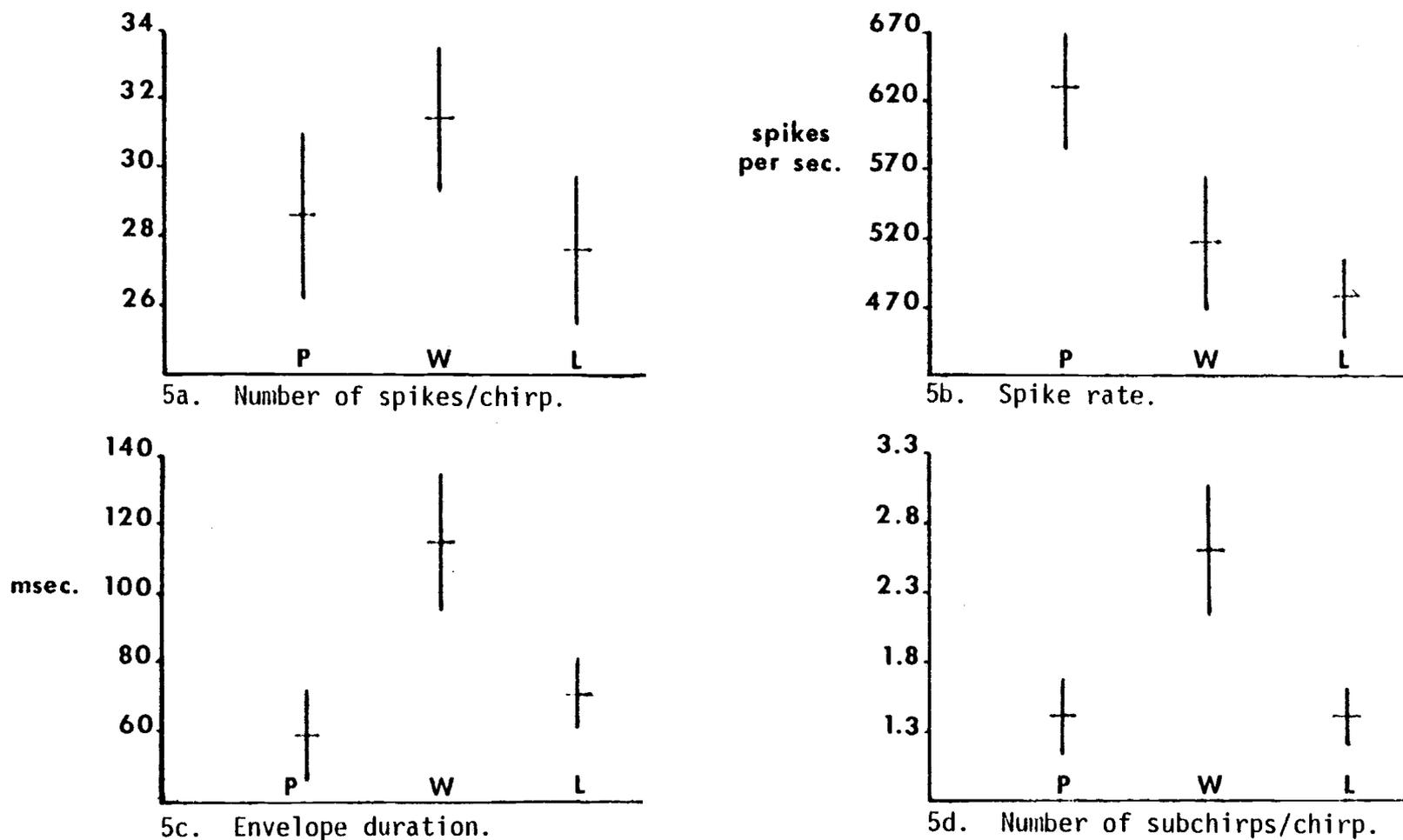
Table 5. Male Stress stridulation: means and standard errors of stridualtion parameters and statistical results of comparisons between samples of D. ponderosae from different hosts and/or years.

Sample	Spikes/Chirp (no.)		Spike Rate (no./second)		Envelope Duration (msec)		n
	$\bar{x}$	SE($\bar{x}$)	$\bar{x}$	SE($\bar{x}$)	$\bar{x}$	SE($\bar{x}$)	
P1978	25.7	1.38	960	23.4	27	1.3	40
WI-III	19.6	0.68	919	18.2	21	0.6	120
L(all)	21.8	0.54	875	16.2	26	0.9	160
L1978	24.7	1.12	802	34.0	32	1.6	40
LI-III	20.8	0.59	899	17.9	25	1.0	120

Comparison	Significance Level of Comparison			
	Mult.	Spikes/ Chirp	Spike Rate	Envelope Duration
P1978 vs. WI-III	0.005	0.0033	NS	0.0033
P1978 vs. L(all)	0.005	0.0167	0.0167	NS
WI-III vs. L(all)	0.005	0.0167	NS	0.0033
L1978 vs. LI-III	0.005	0.005	0.025	0.005
L1978 vs. P1978	0.005	NS	0.025	NS

Figure 6. Means (horizontal lines) and 95% confidence intervals
           (vertical lines) of parameters of male D. ponderosae
           stress stridulation. Males emerged from ponderosa
           (P), western white (W) and lodgepole (L) pine. All
           samples within a host were combined.

6a. Number of spikes/chirp.

6b. Spike rate.

6c. Envelope duration.
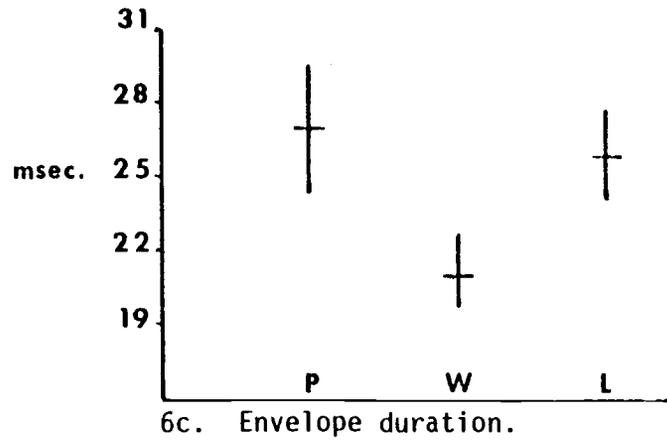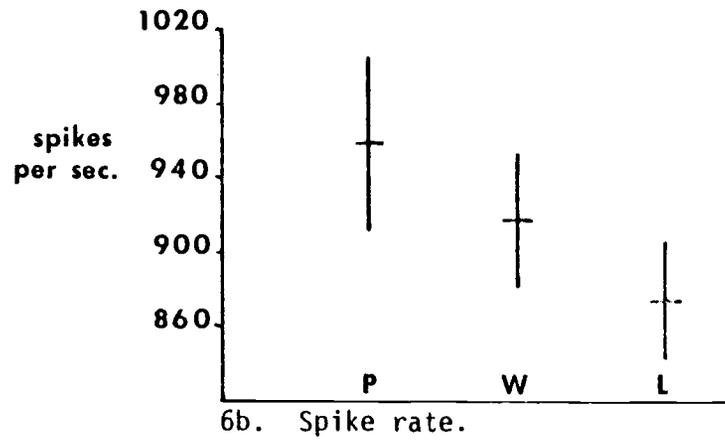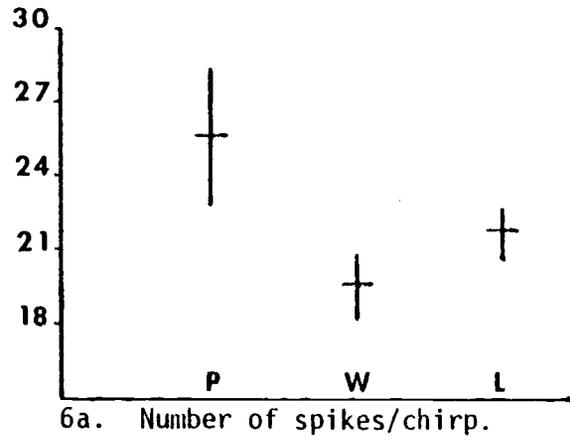
Table 6. Female response to intruder stridulation: means and standard errors of stridulation parameters and statistical results of comparisons between samples of D. ponderosae from different hosts and/or years.

Sample	Spikes/Chirp (no.)		Spike Rate (no./second)		Envelope Duration (msec)		n
	$\bar{x}$	SE($\bar{x}$)	$\bar{x}$	SE($\bar{x}$)	$\bar{x}$	SE($\bar{x}$)	
P1978	6.4	0.38	186	8.8	35	2.1	40
WI-III	8.6	0.47	206	8.8	45	2.5	40
L(all)	7.2	0.36	143	5.6	55	2.9	80
L1978	6.8	0.54	129	6.0	53	3.5	40
LI-III	7.6	0.50	156	9.1	56	4.7	40

Comparison	Significance Level of Comparison			
	Mult.	Spikes/ Chirp	Spike Rate	Envelope Duration
P1978 vs. WI-III	0.005	0.0033	NS	NS
P1978 vs. L(all)	0.005	NS	0.0033	0.0033
WI-III vs. L(all)	0.005	0.0167	0.0033	0.0167
L1978 vs. LI-III	0.005	NS	0.025	NS
L1978 vs. P1978	0.005	NS	0.025	NS

Figure 7. Means (horizontal lines) and 95% confidence intervals
          (vertical lines) of parameters of female D. ponderosae
          response to intruder stridulation. Females emerged from
          ponderosa (P), western white (W) and lodgepole (L) pine.
          All samples within a host were combined.

7a. Number of spikes/chirp.

7b. Spike rate.

7c. Envelope duration.
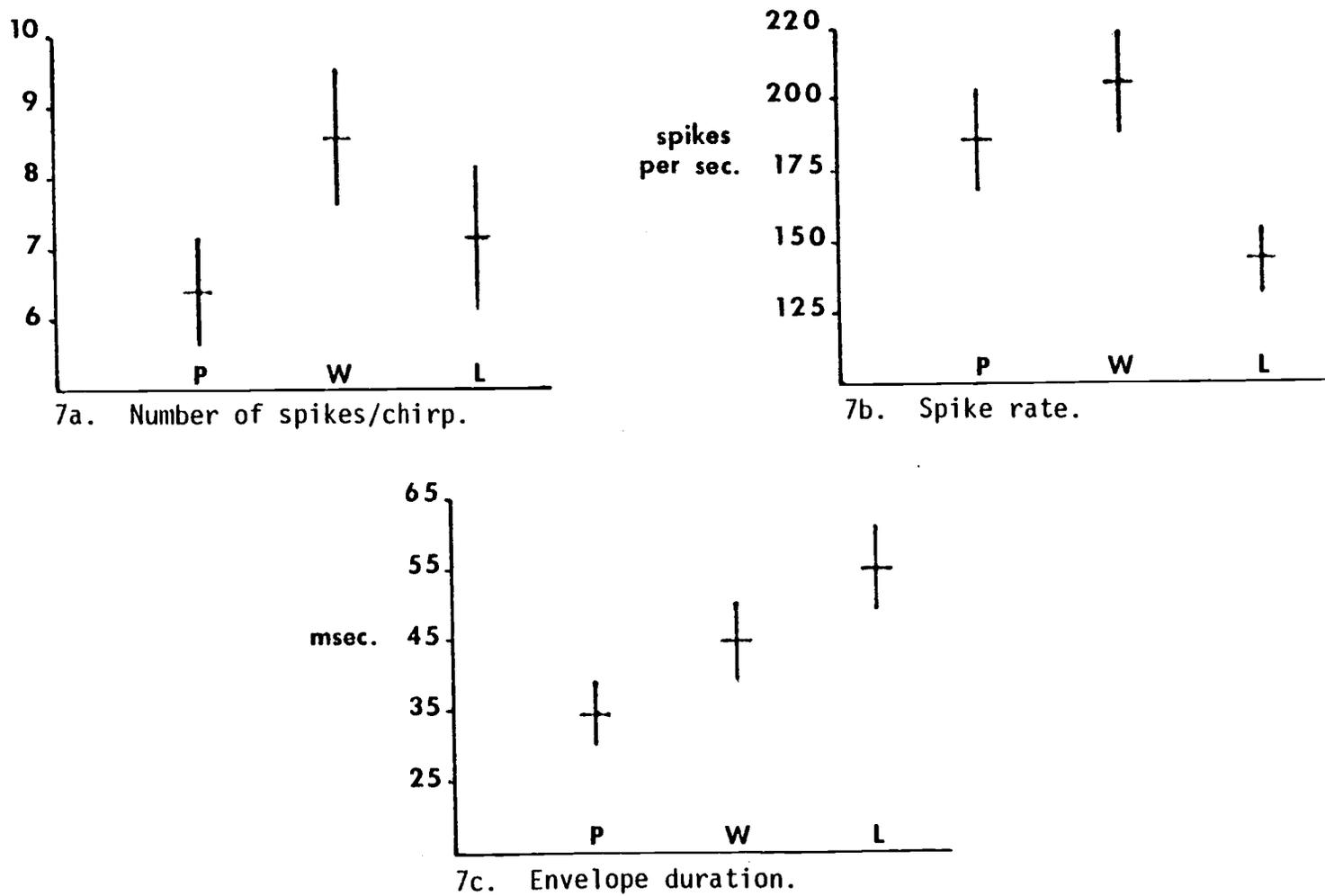
Table 7. Length of left elytron: means and standard errors and statistical results of comparisons between samples of D. ponderosae from different hosts and/or years.

Male Sample	$\bar{x}$ (mm)	SE($\bar{x}$)	n[1]	Female Sample	$\bar{x}$ (mm)	SE($\bar{x}$)	n[1]
P(all)[2]	3.1	0.03	50	P(all)	3.3	0.04	50
WI-III	3.0	0.03	75	WI-III	3.2	0.03	75
L(all)[3]	2.8	0.02	125	L(all)	3.0	0.02	125
P1978	3.1	0.04	25	P1978	3.4	0.04	25
P1979	3.1	0.04	25	P1979	3.2	0.06	25
L1978	2.9	0.04	25	L1978	3.2	0.05	25
L1979[4]	2.8	0.02	100	L1979	3.0	0.02	100

1) Total number of beetles measured (Tables 9-14).
2) Combination of P1978 and P1979 samples (Tables 9-15).
3) Combination of L1978 and L1979 samples (Tables 9-15).
4) Combination of LI-III and LIV-VI samples (Tables 9-14).

Comparison	Significance Level of Comparison	
	Males	Females
P(all vs. WI-III vs. L(all)	0.01[1]	0.01
P(all) vs. WI-III	0.0033	0.0167
P(all) vs. L(all)	0.0033	0.0033
WI-III vs. L(all)	0.0033	0.0033
L1978 vs. L1979	0.025	0.005
P1978 vs. P1979	NS[2]	0.005
L1978 vs. P1978	0.005	0.005
L1979 vs. P1979	0.005	0.005

1) Samples compared significantly different at alpha < 0.01.
2) Samples compared not significantly different (see text for level of significance).

Table 8. Length of pars stridens of left elytron: means and standard errors and statistical results of comparisons between samples of _D. ponderosae_ from different hosts and/or years.

Male Sample	$\bar{x}$ (mm)	SE($\bar{x}$)	n	Female Sample	$\bar{x}$ (mm)	SE($\bar{x}$)	n
P(all)	0.60	0.008	50	P(all)	0.61	0.008	50
WI-III	0.58	0.007	75	WI-III	0.58	0.006	75
L(all)	0.55	0.005	125	L(all)	0.56	0.005	125
P1978	0.62	0.010	25	P1978	0.62	0.010	25
P1979	0.58	0.011	25	P1979	0.59	0.014	25
L1978	0.57	0.009	25	L1978	0.56	0.008	25
L1979	0.55	0.006	100	L1979	0.56	0.006	100

Comparison	Significance Level of Comparison	
	Males	Females
P(all) vs. WI-III vs. L(all)	0.01	0.01
P(all) vs. WI-III	NS	0.0167
P(all) vs. L(all)	0.0033	0.0033
WI-III vs. L(all)	0.0033	NS
L1978 vs. L1979	NS	NS
P1978 vs. P1979	0.025	NS
L1978 vs. P1978	0.005	0.005
L1979 vs. P1979	0.025	NS

Table 9. Number of ridges on elytral pars stridens: means and standard errors and statistical results of comparisons between samples of $\underline{D}$. ponderosae from different hosts and/or years.

Male Sample	$\bar{x}$ (no.)	SE($\bar{x}$)	n	Female Sample	$\bar{x}$ (no.)	SE($\bar{x}$)	n
P(all)	73.9	1.02	50	P(all)	75.9	1.20	50
WI-III	71.8	1.19	75	WI-III	71.3	0.90	75
L(all)	67.8	0.69	125	L(all)	71.4	0.71	125
P1978	77.4	1.19	25	P1978	77.5	1.53	25
P1979	70.4	1.35	25	P1979	74.3	1.84	25
L1978	71.8	1.18	25	L1978	69.5	1.14	25
L1979	66.8	0.78	100	L1979	71.9	0.84	100

Comparison	Significance Level of Comparison	
	Males	Females
P(all) vs. WI-III vs. L(all)	0.01	0.01
P(all) vs. WI-III	NS	0.0033
P(all) vs. L(all)	0.0033	0.0033
WI-III vs. L(all)	0.0033	NS
L1979 vs. L1979	0.005	NS
P1978 vs. P1979	0.005	NS
L1978 vs. P1978	0.005	0.005
L1979 vs. P1979	NS	NS

Figure 8. Means (horizontal lines) and 95% confidence intervals (vertical lines) of length of left elytron (a), length of pars stridens of left elytron (b) and number of ridges of pars stridens of left elytron (c) of D. ponderosae. Beetles emerged from ponderosa (P), western white (W) and lodgepole (L) pine. All samples within a host were combined.
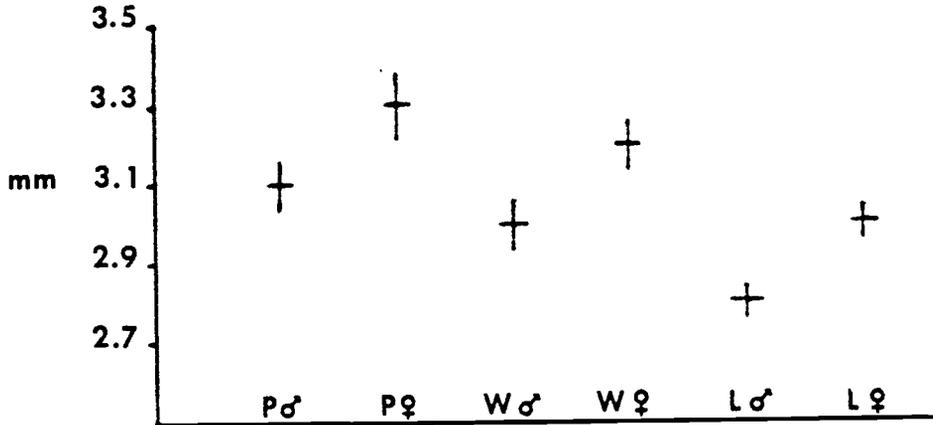
8a.
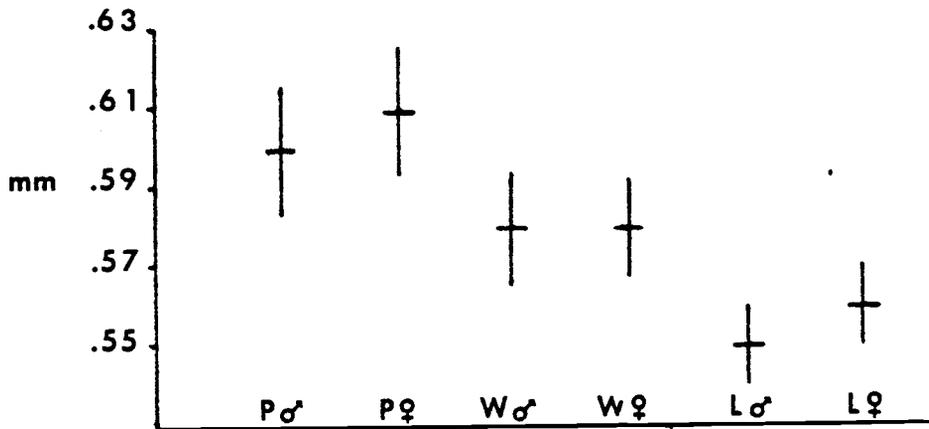
8b.
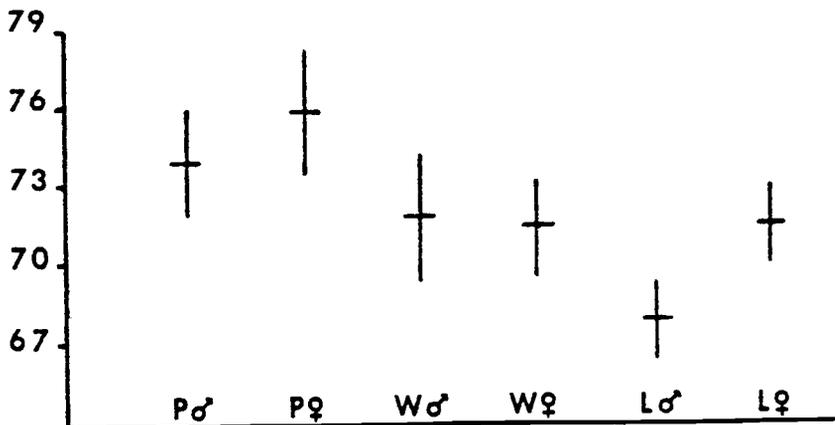
8c.

Table 10. Percentage of ridges in posterior half of elytral pars stridens: means and standard
errors and statistical results of comparisons between samples of <u>D</u>. <u>ponderosae</u> from
different hosts and/or years.

Male Sample	x̄ (%)	SE(x̄)	n	Female Sample	x̄ (%)	SE(x̄)	n
P(all)	41	0.3	50	P(all)	43	0.2	50
WI-III	40	0.2	75	WI-III	43	0.2	75
L(all)	41	0.2	125	L(all)	43	0.1	125
P1978	40	0.4	25	P1978	43	0.3	25
P1979	41	0.4	25	P1979	42	0.3	25
L1978	40	0.4	25	L1978	43	0.2	25
L1979	41	0.2	100	L1979	43	0.2	100

Comparison	Significance Level of Comparison	
	Males	Females
P(all) vs. WI-III vs. L(all)	NS	NS
P(all) vs. WI-III	NS	NS
P(all) vs. L(all)	NS	NS
WI-III vs. L(all)	NS	NS
L1978 vs. L1979	NS	NS
P1978 vs. P1979	NS	NS
L1978 vs. P1978	NS	NS
L1979 vs. P1979	NS	NS

Figure 9. Means (horizontal lines) and 95% confidence intervals (vertical lines) of percentage of ridges in posterior half of elytral pars stridens of D. ponderosae. Beetles emerged from ponderosa (P), western white (W) and lodgepole (L) pine. All samples within a host were combined.
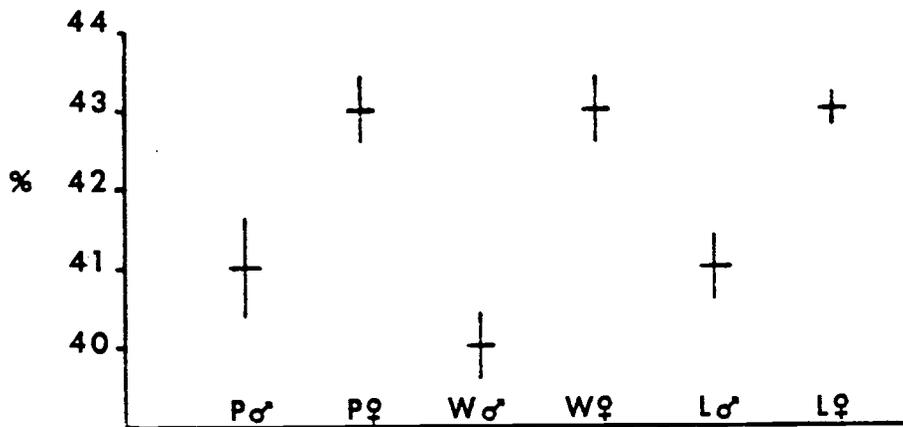
Table 11. Distance between processes of male plectrum: means and standard errors and statistical results of comparisons between samples of D. ponderosae from different hosts and/or years.

Sample	$\bar{X}$ (microns)	$SE(\bar{x})$	n
P(all)	63.0	1.63	50
WI-III	56.0	1.05	75
L(all)	55.7	0.78	125
P1978	67.5	2.30	25
P1979	58.6	1.99	25
L1978	60.8	1.84	25
L1979	54.4	0.82	100

Comparison	Significance Level of Comparison
P(all) vs. WI-III vs. L(all)	0.01
P(all) vs. WI-III	0.0033
P(all) vs. L(all)	0.0033
WI-III vs. L(all)	NS
L1978 vs. L1979	0.005
P1978 vs. P1979	0.025
L1978 vs. P1978	NS
L1979 vs. P1979	NS

Figure 10. Means (horizontal lines) and 95% confidence intervals
            (vertical lines) of distance between processes of the
            plectrum of male D. ponderosae. Beetles emerged from
            ponderosa (P), western white (W) and lodgepole (L)
                pine. All samples within a host were combined.
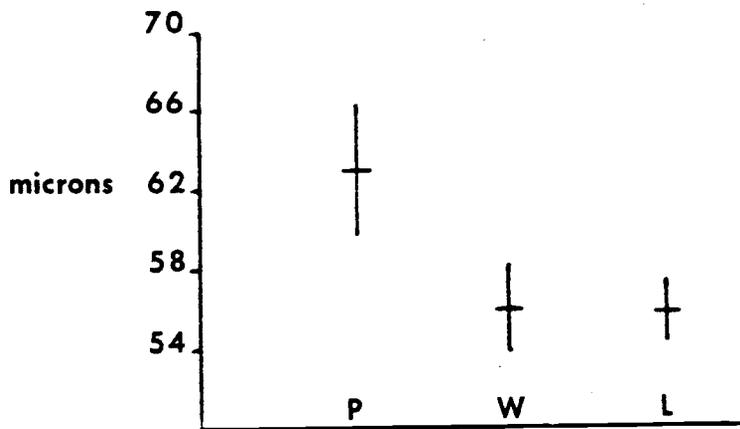
Table 12. Length and number of ridges of sternal pars stridens of female: means and standard errors and statistical results of comparisons between samples of D. ponderosae from different hosts and/or years.

Sample	Length $\bar{x}$ (mm)	SE($\bar{x}$)	n	Number of Ridges $\bar{x}$ (no.)	SE($\bar{x}$)	n
P(all)	o.16	0.004	20	19.8	0.44	20
WI-III	0.15	0.003	30	18.5	0.37	30
L(all)	0.15	0.002	50	17.9	0.36	50
P1978	0.16	0.004	10	20.7	0.42	10
P1979	0.16	0.007	10	19.0	0.68	10
L1978	0.15	0.004	10	18.6	0.54	10
L1979	0.15	0.003	40	17.7	0.34	40

Comparison	Significance Level of Comparison Length	Number of Ridges
P(all) vs. WI-III vs. L(all)	NS	0.01
P(all) vs. WI-III	NS	NS
P(all) vs. L(all)	NS	0.0033
WI-III vs. L(all)	NS	NS
L1978 vs. L1979	NS	NS
P1978 vs. P1979	NS	NS
L1978 vs. P1978	NS	0.025
L1979 vs. P1979	NS	NS

Figure 11. Means (horizontal lines) and 95% confidence intervals (vertical lines) of length (a) and number of ridges (b) of sternal pars stridens of female D. ponderosae. Beetles emerged from ponderosa (P), western white (W) and lodgepole (L) pine. All samples within a host were combined.

11a.

11b.
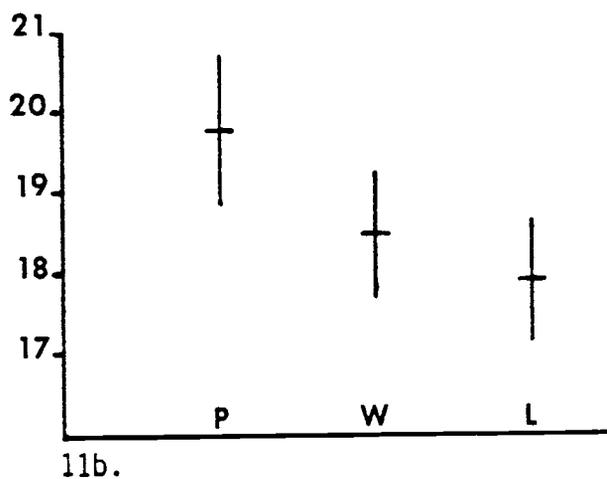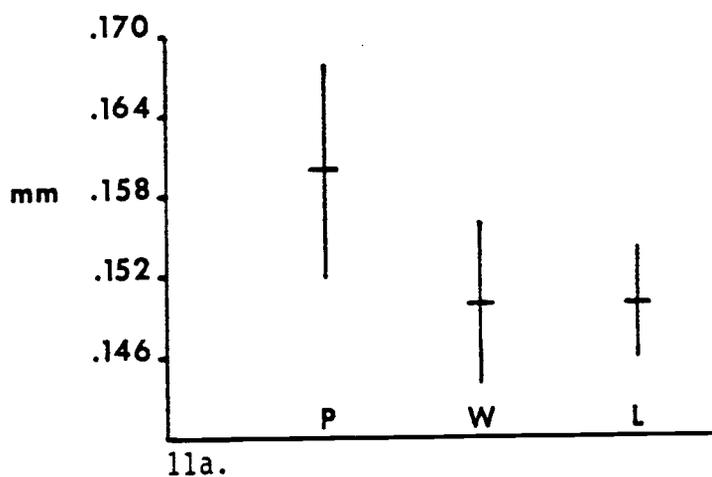
Table 13. Male and female morphology: statistical results of
comparisons between males and females of samples of
D. ponderosae from the same host.

Comparison	Significance Level of Comparison		
	P(all)	WI-III	L(all)
Length of left elytron	0.01	0.01	0.01
Length of elytral pars stridens	NS	NS	NS
Number of ridges on elytral pars stridens	NS	NS	0.01
Percentage of ridges in posterior half of elytral pars stridens	0.01	0.01	0.01

Table 14. Emergence samples: number of beetles emerged, percent males in total number emerged, emergence density and average billet diameter.

Sample	Number Emerged	Percent Males	Emergence Density (beetles/m^2)	Average Billet Diameter (m)
P1978	700	28.3	42	0.23
P1979	692	31.5	130	0.22
P(all)[1]	1392	29.9	64	0.23
L1978	2198	35.8	912	0.23
LI-III	1069	36.8	248	0.26
LI	537	35.2	266	0.28
LII	282	32.6	221	0.22
LIII	250	45.0	159	0.28
LIV-VI	1273	32.8	310	0.26
L(all)[1]	4540	35.4	419	0.25
WI	2601	49.1	1146	0.22
WII	125	48.0	31	0.30
WIII	3352	47.0	1004	0.28
WI-III[1]	6078	47.9	632	0.27

1) Indicates that all samples within a host species were combined to give overall figures.

Table 15. Percentages of males in first and second
halves of total emergence.

Sample	First Half	Second Half
P1978 (subsample)	26.79	34.34
P1978 (subsample)	20.74	33.33
P1979	28.61	34.39
L1978	35.21	36.31
LI	27.06	43.27
LII	24.44	40.66
LIII	37.50	52.50
LIV-VI	28.16	36.10
WI	50.38	47.89
WII	46.77	49.21
WIII	46.00	47.97

Table 16. Analysis of variance tables: percentages of males
in first and second halves of total emergence.

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F
Ponderosa				
Total	5	146.640		
Treatment	1	111.974	111.974	12.92*
Error	4	34.666	8.666	
Lodgepole				
Total	9	624.675		
Treatment	1	318.886	318.886	8.34*
Error	8	305.789	38.224	
White				
Total	5	12.646		
Treatment	1	0.614	0.614	0.20
Error	4	12.032	3.008	

* Indicates significant difference between treatments at alpha < 0.05.

Table 17. Analysis of variance table for regression of hourly emergence on temperature and temperature squared variables.

Source	Degrees of Freedom	Sum of Square	Mean Squares	F
Total	204	53.1700		
Regression	2	14.5760	7.28799	38.14**
Residual	202	38.5940	0.191060	

R^2 = 0.2741

** Indicates the regression is significant at alpha < 0.01.

Table 18. Analysis of variance table for regression of hourly emergence on day, day squared, and day cubed variables.

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F
Total	204	53.1700		
Regression	3	12.6621	4.22071	20.94**
Residual	201	40.5079	0.201532	

R^2 = 0.2381

** Indicates the regression is significant at alpha < 0.01.

Table 19. Analysis of variance table for regression of hourly
emergence on temperature, temperature squared, day,
day squared, and day cubed variables.

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F
Total	204	53.1700		
Regression	5	29.6014	5.92029	49.99**
Residual	199	23.5686	0.118435	

R^2 = 0.5567

** Indicates the regression is significant at alpha < 0.01.

DISCUSSION

Douglas-fir beetle (Dendroctonus pseudotsugae) males have been shown to distinguish between chirps of females and males of the same species (Rudinsky et al., 1976). Female Douglas-fir beetles are able to discriminate between attractant and stress chirps of the males (Rudinsky and Michael, 1972). Therefore, it is not unreasonable to expect that the mountain pine beetle can discriminate between the several, distinct sonic signals it has evolved (Ryker and Rudinsky, 1976). If mountain pine beetle stridulation has a species or population recognition function acting to ensure that beetles from one pine host pair and mate with beetles from the same host, then the male attractant chirp would seem most likely to show host-specific differences. Because D. ponderosae females tend to reject silenced males, Ryker and Rudinsky (1976) suggested that the attractant chirps emitted by the males while digging into the frass at the entrance of a female's gallery serve a species recognition function. A courtship chirp, distinct from the male attractant chirp, has been reported for D. ponderosae males (Ryker and Rudinsky, 1976); however, courtship chirping occurs only after pair formation. Indeed, all males that were not ejected in the first few minutes after they entered a female gallery, before courtship chirping began, subsequently mated (Ryker and Rudinsky, 1976). Thus, if mountain pine beetle pairing is dependent on female recognition of an appropriate male sonic signal, the male attractant chirp is the only likely candidate.

On the basis of the present study, however, no such interhost recognition function can be ascribed to male attractant chirping. The

attractant chirping of beetles from different hosts was highly similar despite the fact that the chirping behavior in other contexts differed significantly between beetles from different hosts or between beetles from different subspecies of the same host. Furthermore, beetles from any two of the three hosts considered in this study are able to pair and mate (Lanier and Wood, 1968; personal observation) indicating that, if differences do exist in the attractant chirping of males from different hosts, they are not sufficient to prevent the females from recognizing the male as a conspecific and permitting his entry into her gallery. The similarity of the attractant chirping behavior of the males of all three hosts seems to indicate a tight genetic control of this behavior. This conforms to the idea that the attractant chirp serves, or has served, a species recognition function. Deviation in a male's attractant chirp from the form readily recognized by the female could conceivably lead to delay in his acceptance by the female, thus increasing the possibility of predation or of interference by a rival male, or the male's rejection. This could be investigated using silenced males and synthesized attractant chirping, varying the signal to see how the change in stridulation parameters affects pairing behavior.

In contrast to the male attractant chirping, D. ponderosae stridulation in the other three behavioral contexts differed greatly between beetles of various samples. As indicated by the coefficients of variation of individual parameters, the amount of variation within a sample generally was greater for male rivalry stridulation and for the female chirp than for the attractant chirping in the same sample

(Appendix 1). It may be that these signals, if they do indeed function as signals, convey the message simply by being emitted in some general form in the correct behavioral context and that tight genetic control is not required. The female chirp may function to convey the fact of her presence to intruders or nearby females simply by its being detected in any reasonable form; male rivalry chirping may function in an analagous manner to signal the presence and aggressive intent of the emitter. Ryker and Rudinsky (1976) have shown that mountain pine beetle rivalry stridulation is accompanied by other aggressive behaviors, such as biting and butting, which would be sufficient to convey an aggressive intent but which are certainly more dangerous to both emitter and receiver than a more ritualized form of competition involving acoustic intimidation.

The function of the simple stress chirp of male D. ponderosae is unknown. The sound or vibrations created by the chirp may startle a potential predator and aid in a beetle's escape (Arrow, 1942). These short chirps with their dense spike rates may be more effective than the slower, less dense interrupted chirps in this regard, but it is difficult to imagine selective pressures leading to a very tightly controlled form of this chirp. The stress chirp, along with the male rivalry and female chirps, may be more dependent on individual beetle morphology or its physiological state than on its genetic makeup as compared to male attractant stridulation.

Other studies have reported morphological differences betwen mountain pine beetles from different infestations (McGhehey, 1971) and from different hosts (Hay, 1956; Sturgeon, 1980). Therefore, it was

expected that differences in morphology would exist between beetles
from the various samples in the present study and, in all comparisons
made, differences did indeed exist.

In the present study, in all cases where differences in
morphology existed between beetles from ponderosa and beetles from
either white or lodgepole pine, the means for the ponderosa beetles
were larger. The morphology means for the white pine beetles were, in
all cases where significant differences existed, larger than the means
for the lodgepole beetles. Hay (1956) also found that Dendroctonus
monticolae (= ponderosae) from ponderosa pine were larger than D.
ponderosae from lodgepole pine. This is in contrast, however, to the
work of Sturgeon in Colorado who found no morphological differences
between mountain pine beetles from ponderosa and lodgepole, though
beetles from both these hosts were larger than beetles from limber
pine (Sturgeon, 1980). Sturgeon (1980) reported also that the length
of the left elytron was not a useful character in discriminating
between beetles of different hosts. However, in the present study, in
the L1978 versus P1978 and L1979 versus P1979 comparisons of beetles
from sympatric hosts and from the same year, the means for the lengths
of the left elytron were significantly different and were consistent
with differences in the other morphological characters between beetles
from the two hosts. Furthermore, more differences were found in the
comparisons of the left elytron than in any other character measured;
differences in the length of the left elytron did not necessarily
correlate with differences in the stridulatory apparatus. The
structure of the stridulatory apparatus may be less subject to

environmental influences as determined by host and geographically related differences and may be more subject to genetic control than is overall size.

As previously reported (Hay, 1956; Sturgeon, 1980), female mountain pine beetles were greater in overall size than the males. In the present study, as indicated by the length of the left elytron, this was true of every sample taken though only the samples grouped by host tree were compared statistically. This difference in size between males and females was not found in the length of or number of teeth in the elytral pars stridens, with the single exception that female D. ponderosae from lodgepole had more teeth on the elytral file than did the males. These results contrast with the work of Michael and Rudinsky (1972) and Rudinsky and Michael (1973) whose results indicated that, for four species of Dendroctonus, including D. ponderosae, the elytral files of the females were shorter and contained fewer teeth. These previous results were not analyzed statistically and were based on a sample size of ten beetles per species. The results of this study should be considered more accurate due to greater sample sizes.

Stock and Guenther (1979) and Stock and Amman (1980) have previously reported greater degrees of genetic variation between males of different populations than between females of these populations. In the present study relatively more morphological differences were detected between males of different populations (19 of 35 statistical comparisons made resulted in significant differences) than between females (15 of 42 statistical comparisons resulted in significant

differences). Stock and Guenther (1979) suggested that greater

genetic divergence may occur among males due to their greater suscep-

tibility to stress than females (Amman and Pace, 1976; Safranyik,

1976), resulting in divergent selection which would operate more

strongly on males of different populations than on females.

Many host factors could conceivably influence beetle morphology

by affecting the suitability of the host for beetle survival and/or

growth. Tree size is known to affect beetle attack behavior and

survival (Cole and Amman, 1969; Roe and Amman, 1970; Geiszler and

Gara, 1978). Bark thickness is known to be important in the spatial

arrangement and the frequency of attacks by the mountain pine beetle

(Safranyik and Vihayasai, 1971; Evenden et al., 1943) and also has an

effect on subcortical temperatures, which most certainly affect beetle

survival (Powell, 1967). Phloem thickness is known to affect beetle

size (Amman and Pace, 1976) and also affects survival (Amman, 1972)

with more and larger adults surviving on the average in a tree with

thick phloem as opposed to a tree with thinner phloem. Differences in

terpene constituents between hosts are known to exist (Mirov, 1961)

and Smith (1963, 1965) has shown species-specific differences in the

effects of different terpenes on Dendroctonus beetles. Host terpenes

might act either directly on the beetle or indirectly on their

associated fungi and other organisms (Shrimpton, 1978) by reducing the

quality or availability of the beetles' food supply, thereby effecting

beetle morphology.

The sex ratio results are more or less consistent with results

from other studies. McGhehey (1969) reported that 35.8% of the

beetles emerging from lodgepole in one study were males. Other

figures cited for mountain pine beetles emerging from lodgepole are

33.3% (Reid, 1958), 25.6% (Rasmussen, 1974) and 28.1 to 38.9% (Amman

and Pace, 1976). Studies of mountain pine beetle emergence from

ponderosa have resulted in average percentages of males varying from

27% for the first two weeks of emergence (Billings and Gara, 1975) to

42% for the final two weeks (Gray et al., 1972). The percentage of

males in the total number of mountain pine beetles from western white

pine has been reported as 50% (DeLeon et al., 1934) and 33.3%

(Billings and Gara, 1975). The reason for this reported variation in

the sex ratio of mountain pine beetle broods in white pine is unclear

but likely reflects varying host conditions or brood densities which

could act to stress the developing larvae and cause differential

survival of the sexes, favoring the females (Cole, 1973, 1975; Amman   ·

and Pace, 1976).

Rasmussen (1980) reported that the percentage of female mountain

pine beetles from lodgepole pine first rose and then declined over the

emergence period during both years of a two year study. Billings and

Gara (1975) noted that the sex ratio changed in favor of males in

mountain pine beetle emergence from ponderosa pine in Washington; no

such shift occurred in the sex ratio of beetles emerging from white

pine. The results of the current study concur with these previous

results. Scolytus multistriatus has been shown to exhibit a similar

change in the sex ratio in favor of males (Bartels and Lanier, 1974).

The reason for this is unknown. It may, however, be of advantage to

mountain pine beetle individuals in that, with the relatively faster

development and/or emergence rate of the females, more are available during the beginning of the emergence period to join in a mass attack and assist in overcoming the host tree defenses.

Previous studies have shown that female mountain pine beetles survive better than males under stress (Amman and Pace, 1976; Safranyik, 1976). Of the factors which might be expected to induce stress and thus decrease the proportion of males, evidence exists that crowding, through its effects on food supply and/or developmental period, may act to create differential mortality of males and females (Cole, 1973, 1975) and that phloem thickness may have an effect with males surviving proportionally less in thin-phloemed trees than females (Amman and Pace, 1976; Amman, 1978). Whether either of these factors, either singly or in conjunction, are responsible for the differences between the proportion of males in lodgepole and ponderosa emergence and the proportion of males in white pine emergence cannot be determined from the present study. However, large differences in emergence density within a host species seemed to have little predictable effect on the sex ratio. Furthermore, the highest percentages of males were found in white pine where the emergence densities were both greatest and lowest.

Other studies have reported varying densities for mountain pine beetle emergence. Amman (1969) found the number of emergence holes per ft^2, a measure which is significantly correlated with emergence density (Reid, 1963), to vary from 0 to 120 in one study on lodgepole. Amman (1972) reported emergence densities from lodgepole varying from $0/ft^2$ to $100/ft^2$, and Amman and Pace (1976) reported approximately

the same figures for beetles emerging from lodgepole in a separate study. Klein et al., (1978) reported that the number of emergence holes per ft^2 during a 7 year lodgepole infestation study peaked at 32.8 the second year and fell to a low of less than 2 the final year, which coincided with a decrease in the killing of the large-sized trees (due to decreasing availability) over the course of the infestation. For mountain pine beetles emerging from ponderosa, McCambridge (1964) reported emergence densities of 21.5 to 45.6 beetles/ft^2 and Schmid (1972) reported densities of 16 to 31/ft^2. Emergence densities in the present study are in line with previously reported figures, showing wide variation but with the lodgepole figures being higher than the ponderosa figures, which is true of the highest figures in the previous studies. The low emergence density in the WII sample could have resulted from felling that tree in the fall, resulting in premature and excessive drying of the phloem region or in abnormally low temperatures and resultant mortality due to its overwintering on the ground. Brood production and subsequent emergence density may be affected by or correlated with a number of factors. Among these are phloem thickness and egg gallery density (Amman and Pace, 1976), the number and size of pitch pockets (Amman, 1972), tree diameter (Cole and Amman, 1969), bark thickness (Amman, 1969) and parasites, predators, pathogens, temperature extremes and drying (Cole, 1975). Whether the differences in emergence densities in the present study reflect actual host differences was not determined.

A number of experimenters have found the emergence of D.
ponderosae to be rhythmic to some degree. Watson (1970) found that
emergence from lodgepole under constant temperature conditions was
rhythmic (possibly circadian) with hourly emergence tending to be
greater between the hours of 6:00 a.m. and 2:00 p.m. than at other
times. Billings and Gara (1975) reported that hourly emergence from
ponderosa in the field was rhythmically controlled and asynchronous
with ambient temperature with emergence being greatest between the
hours of 8:00 a.m. and 1:00 p.m. They further reported that mountain
pine beetle hourly emergence from white pine exhibited a similar diel
periodicity, but that maximum emergence was closely synchronous with
maximum temperature.

Results from the present study agree closely with these previous
studies. Sturgeon (1980) suggested that allochronic separation of
broods from different hosts may act to restrict gene flow and increase
the rate of accumulation of host-adapted genes. Differences in the
time of emergence and flight during the day, especially if accompanied
by diel periodicity of pheromone emission and/or receptivity could
also act to restrict gene flow between individuals from different
hosts. Beetles from all three hosts do, however, emerge and fly
throughout the daylight hours when temperatures are suitable in Oregon
populations (personal observation).

The effects of temperature in the regression equations correspond
well with previously reported results. Gray et al. (1972) reported
that no mountain pine beetle emergence occurred from ponderosa below
16°C and Billings and Gara (1975) reported this same lower limit for

emergence of D. ponderosae from both ponderosa and white pine. Both Gray et al. (1972) and Billings and Gara (1975) reported that emergence began to decrease at temperatures above 30°C in their studies with ponderosa and white pine respectively. Rasmussen (1974) found reduced mountain pine beetle emergence from lodgepole at temperatures exceeding 32°C.

Mountain pine beetle emergence has been observed under conditions of cold storage at 3°C in the laboratory (personal observation). This has been observed mainly late in the summer during the latter portion of, or entirely after, the normal emergence period for this species. Emergence may be partially subject to some annual rhythm that acts to ensure that an individual maturing late in the emergence period will be able to emerge and reproduce though conditions are not ideal for emergence. Such a mechanism would also explain the prediction of the emergence regressions of increasing hourly emergence late in the emergence period.

Genetic differences between mountain pine beetle populations have been associated with host tree differences (Stock and Amman, 1980; Sturgeon, 1980) and geographic differences (Stock and Guenther, 1979, Sturgeon, 1980). Differences in other insect species have been attributed to discrepancies in the phase of the infestation (Turner, 1960). In some of the comparisons made in this study, geographic differences are confounded with host differences and the two cannot be separated. But if the mountain pine beetle does mate at random with respect to host tree then the differences between the L1978 and P1978 samples and between the L1979 and P1979 samples could be genuine host-

related differences, since differences in geographic influences and the stage of infestation would not likely exist. In the present study a greater number of significant differences in morphology was found between lodgepole and ponderosa D. ponderosae samples taken the same year and from proximate locations than was found in comparisons of beetles from the same host species but from different years and geographically separated locations.

The genetic identity indices from studies of genetic variation among populations of D. ponderosae (Stock and Guenther, 1979; Stock and Amman, 1980; Sturgeon, 1980) are in line with what might be expected to occur among local populations of a single species (Ayala, 1975); and Wood (1982) has concluded that, though genetic divergence among local populations of D. ponderosae has occurred or is occurring, the degree of divergence is not such that "geographical races can be recognized". In the present study no differences existed among beetles of different hosts in male attractant stridulation, although significant differences did exist between samples from different hosts and from two subspecies of lodgepole in male rivalry, male stress and female response to intruder stridulation behavior. Significant differences in morphology were detected as well among beetles from different hosts or from the same host but from different locations and years. Significant differences in emergence behavior existed between beetles from ponderosa and lodgepole, on one hand, and from western white pine, on the other. The morphology and emergence differences that existed are consistent with differences detected in other studies. It is not known whether such differences as those detected

by this study are a direct result of host tree differences or whether they are the result of the genetic divergence of populations of D. ponderosae selectively infesting the various pine hosts or whether both factors are partially responsible. The variation among populations of D. ponderosae detected in the present study and in other studies do suggest that divergence has occurred among populations of the mountain pine beetle but do not indicate that there is currently any mechanism that could result in reproductive isolation among populations from different host species.

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Appendix 1. Coefficients of variation of stridulation parameters

Parameter	Behavioral Context			
	Male Attractant	Male Rivalry	Male Stress	Female Response to Intruder
P1978				
Spikes/Chirp	31.2	26.2	32.1	37.5
Spike Rate	16.3	20.2	15.4	29.9
Envelope Duration	30.8	68.6	30.8	37.0
Subchirps/ Chirp	25.3	59.2		
W1979				
Spikes/Chirp	26.3	20.3	37.8	49.3
Spike Rate	24.6	29.7	21.7	38.1
Envelope Duration	30.7	53.0	28.9	49.2
Subchirps/ Chirp	28.6	54.6		
L(all)				
Spikes/Chirp	25.6	35.3	31.3	45.6
Spike Rate	19.7	26.5	23.4	35.2
Envelope Duration	31.9	60.7	42.0	47.7
Subchirps/ Chirp	24.3	64.3		
L1978				
Spikes/Chirp	39.0	37.3	28.8	50.0
Spike Rate	19.6	23.2	26.8	29.2
Envelope Duration	27.0	66.6	32.1	41.3
Subchirps/ Chirp	25.7	70.7		
LI-III				
Spikes/Chirp	19.7	19.5	31.1	41.5
Spike Rate	19.7	25.2	21.8	36.9
Envelope Duration	33.4	45.7	43.6	53.4
Subchirps/ Chirp	24.1	36.8		