

AN ABSTRACT OF THE THESIS OF

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Title: SOUND PRODUCTION IN THREE SYMPATRIC IPS  
COLEOPTERA:SCOLYTIDAE) SPECIES CO-INHABITING SITKA  
SPRUCE (PICEA SITCHENSIS)

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✓ Julius A. Rudinsky /

Three sympatric species of Ips, colonizing Sitka spruce, were investigated with regard to their infestation habits, stridulating apparatus and acoustic signals. The above phenomena are evaluated qualitatively and/or quantitatively and the acoustic signal differences are proposed as a possible factor for maintaining species isolation, although function is not shown.

Field and laboratory observations show that I. concinnus and I. tridens tridens have similar microhabitat preferences, emergence periods, brood development and pairing behavior. Although field observations were not obtained for I. plastographus, previous studies indicate that their ecological and attack behavior is probably similar to the two other species.

Statistical comparisons of measured parameters of the male and female I. concinnus gular-prosternum stridulatory organ revealed

several intra-specific differences, which, in several parameters, were correlated with beetle size. Utilization of the electron microscope and compound light microscope did not reveal any discernible stridulatory organs on male and female I. t. tridens beetles. Electron micrographs and measurements of length, width and number of ridges are presented for the vertex-pronotum stridulatory organs on female I. plastographus. Stridulatory structures were not found on male I. plastographus. The stridulatory structure differences encountered in the three species are considered a major influence in acoustic signal disparities.

Stridulations produced by I. concinnus beetles in the behavioral contexts of attraction, female stress and male aggression are illustrated and statistically compared, using the parameters of pulse number per chirp, chirp duration and pulse rate. I. concinnus attraction stridulations, tape recorded as five consecutive females join a male, show that the chirps of the first female differ statistically from chirps of following females in number of pulses per chirp. Additionally, pulse rate and duration of chirps of only the third female differed significantly from chirps of the first female. These stridulation differences appear to be correlated with attack behavior and increasing male resistance to entering females as number of females increases in the nuptial chamber.

Although the brief clicks emitted by male and female I. t. tri-  
dens males in an attraction context are similar to male aggression and  
female stress clicks, they are distinctly different in structure, dura-  
tion and frequency when compared to I. concinnus and I. plastographus  
attraction chirps.

Oscillographs of stridulations produced by female I. plasto-  
graphus in the natural behavioral contexts of attraction, rivalry and  
stress are presented. Statistical comparisons show that attraction  
chirps are quicker in pulse rate and that rivalry chirps possess a  
greater number of interrupted chirps.

Attraction chirps of I. concinnus and I. plastographus are  
statistically compared and appear distinct on the basis of chirp dura-  
tion and pulses per chirp. Oscillograms depicting internal pulse  
structure of chirps reflect stridulatory apparatus differences between  
I. concinnus and I. plastographus. Pulse structure as an important  
facet of intra-specific signal recognition is discussed.

The distinctiveness of each species' attraction stridulations and  
the apparent importance of acoustic signals in pairing behavior sug-  
gests that stridulation contributes to reproductive isolation in these  
three species of Ips.

Sound Production in Three Sympatric Ips  
(Coleoptera: Scolytidae) Species Co-inhabiting  
Sitka Spruce (Picea sitchensis)

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SOUND PRODUCTION IN THREE SYMPATRIC IPS  
(COLEOPTERA: SCOLYTIDAE) SPECIES CO-INHABITING  
SITKA SPRUCE (PICEA SITCHENSIS)

I. INTRODUCTION

Beetles in the family Scolytidae breed in the cryptic micro-environment between bark and sapwood (bark beetles) or in the sapwood itself (Ambrosia beetles). Using powerful aggregation pheromones, pioneer beetles attract large numbers of both sexes to a host tree enabling rapid mass invasion and a complete exploitation of available food material (Borden and Stokkink, 1971; Birch, 1975). Because a few species aggressively colonize recently felled or living trees, especially commercially desirable North American species, several economic pests are recognized (Davidson and Prentice, 1967). The interaction of chemical and acoustic communication appears an integral part in the process of bark beetle pair formation and host colonization (Rudinsky, 1968, 1969; Rudinsky and Michael, 1972; Rudinsky et al., 1976), particularly in the two most important bark beetle genera, i.e. Dendroctonus and Ips.

In the animal kingdom communication can be defined as the transfer of information from one organism to another that adaptively alters the probability pattern of behavior in the receiving organism (Frings and Frings, 1964; Alexander, 1967; Wilson, 1971). The transfer of information is accomplished through the media of light

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waves, chemicals, sound waves or substrate vibrations (Alexander, 1967), the mechanism of which has developed through natural selection (Frings and Frings, 1964; Otte, 1974). The present study describes the sound production apparatus and acoustic signals of three sympatric Ips species and proposes its use in species isolation, although communicative function was not ascertained.

Recent reviews of acoustic communication have resulted in a unification of arthropod sound production research, acoustic methodology and associated acoustic behavioral terminology (Haskell, 1961; Busnel, 1963; Alexander, 1967). In an admittedly incomplete bibliography, Frings and Frings (1960) cite 1752 publications dealing with arthropod sound production and its reception. Sound production in insects most commonly occurs when two specialized structures are rubbed together, termed stridulation (Dumortier, 1963), or tymbal organs pulsate rhythmically (Frings and Frings, 1958). Among the many families of arthropods the singing Orthoptera and Homoptera have received predominant attention (Alexander, 1967). Studying two sympatric grasshopper species (Chorthippus brunneus Thunb. and C. biguttulus L.), Perdeck (1958) concluded that prevention of hybridization in nature is exclusively maintained through species specific song reactions. Sympatric species in the families Gryllidae (Orthoptera) and Cicadidae (Homoptera) are known to discriminate between species for mating purposes using species specific sounds (Alexander and Moore, 1958; Walker, 1957).

The occurrence of stridulatory organs and sound production has been documented for many species of Coleoptera (Gahan, 1900; Arrow, 1904). Although the functional relationships of sound production have remained somewhat obscure among the majority of Coleoptera, functions have been implied on the basis of behavioral context alone (Haskell, 1961). Aggressive and/or courtship sounds are known for beetles and include the families Passalidae (Schuster and Schuster, 1971), Cerambycidae (Michelsen, 1966), Trogidae (Alexander et al., 1963), Hydrophilidae (Van Tassel, 1965; Ryker, 1972, 1975, 1976), Scolytidae (Wilkinson et al., 1967; Barr, 1969; Rudinsky and Michael, 1972, 1973; Michael and Rudinsky, 1972; Rudinsky et al., 1974; Libbey et al., 1974; Oester and Rudinsky, 1975; Rudinsky and Ryker, 1976; Ryker and Rudinsky, 1976a, b; Swaby and Rudinsky, 1976), and Geotrupidae (Winking-Nikolay, 1975). Van Tassel (1965) described stress chirps of 12 species of Hydrophilidae and, in four of these species, analyzed premating acoustic signals (tremolos). The tremolos appeared more distinct for each species than the stress chirps, and it was hypothesized that premating stridulation may be an important isolating mechanism where species overlap in the genus Berosus. Recent experimental evidence indicates that two sympatric species of Tropisternus can hear water-transmitted sounds and males can discriminate their specific female calling chirps from other conspecific stridulations (Ryker, 1975).

Studies of scolytid stridulation and/or stridulatory organs have been reviewed and grouped into three main categories (Barr, 1969): (1) location and structure of stridulatory organs; (2) original observations of stridulation or sound production; and (3) usefulness of stridulatory organs or sounds as a characteristic in secondary sex determinations. Ninety-three species of European and North American bark beetles are known to stridulate or produce stridulation (Barr, 1969). Of the 33 species in the genus Ips, 16 possess stridulatory organs while the remaining 17 species appear to lack a stridulatory apparatus (Barr, 1969). The two stridulatory structures involved are distinct: the "plectrum" or scraper and the "pars stridens" or file. The pars stridens is considered a more complex organ and may consist of spines, tubercles, teeth, hair or ridges, whereas the plectrum is usually composed of a sharp edge or tooth (Dumortier, 1963). The plectrum is rubbed on the pars stridens which vibrates to produce sound. Stridulating Ips species possess a vertex-pronotum or a gula-prosternum type of stridulatory mechanism. Both organs of the vertex-pronotum type are complex ridged structures, while the gula-prosternum type consists of a somewhat crude, multiple ridged pars stridens and a single ridge for the plectrum.

Males of several destructive species of Dendroctonus produce a species specific acoustic response when stimulated by their respective attractive female frass (Michael and Rudinsky, 1972; Rudinsky

and Michael, 1974; Rudinsky et al., 1974). Until recently (Rudinsky and Michael, 1973; Oester and Rudinsky, 1975), the first attacking sex among Scolytidae, i.e. male Ips and female Dendroctonus, was considered silent (Barr, 1969). Additionally, research has elucidated a complex sequence of olfactory and sonic responses between male and female D. pseudotsugae Hopk. which results in both sexes contributing to the inhibition of the flying population, thus preventing over-colonization of the host (Rudinsky et al., 1976).

In experiments where the female stridulatory organs of Ips calligraphus (Germar) and Ips paraconfusus Lanier (= confusus LeC) were surgically removed, males of the respective species vigorously repelled or exhibited greater resistance to females attempting entry into an attractive male gallery (Wilkinson et al., 1967; Barr, 1969). This is evidence that female stridulation may be necessary for species recognition and/or conspecific cohesion during pair formation in Ips. In the first descriptive statistical comparison of Ips stridulation in several behavioral contexts, Swaby and Rudinsky (1976) found that Ips pini (Say) stress stridulations have double the number of pulses per chirp and a slightly faster pulse rate as compared to rivalry or attraction stridulations, although overlap of ranges was apparent. Through implementation of parallel acoustic and olfactory experiments, no correlation between changes in female attraction

chirps and changes in attraction response was apparent in I. pini (Swaby and Rudinsky, 1976).

Ips concinnus (Mannerheim) and Ips tridens tridens (Mannerheim) commonly attack Sitka spruce, Picea sitchensis (Bong.) Carr., and are distributed along a narrow Pacific Coast belt from northern California to southern Alaska (Chamberlin, 1939). Little information exists on the biology of I. t. tridens or I. concinnus; available field observations are generalized and describe gallery patterns, maximum number of female egg galleries present for each male nuptial chamber and seasonal emergence and development patterns (Chamberlin, 1939; Bright and Stark, 1973).

Ips plastographus (LeConte) normally is not found inhabiting Sitka spruce, but was found on this host in small numbers<sup>1</sup> during the spring of 1974. Typically, I. plastographus follows the distribution of Pinus contorta Dougl. from southern California to southern British Columbia and south in the Rocky Mountains to Yellowstone National Park (Lanier, 1970). This species usually attacks and breeds in the upper portion of prostrate trees and is atypical in its habit of constructing 1-3 cm tunnels in the xylem where the teneral adults can move in and out (Johnson, 1954; Lanier, 1967, 1970). In the southern

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<sup>1</sup> A larger series is necessary to fully determine the subspecies, S.L. Wood, personal communication.

part of its range egg galleries are initiated in May or early June, extending through August (Bright and Stark, 1973). Re-emergence of originally attacking adults occurs two or three successive times as fresh host material is utilized.

Other than general statements on presence of stridulatory structures, acoustic information is lacking for I. concinnus, I. t. tridens and I. plastographus (Barr, 1969). This study represents a preliminary investigation of the acoustic behavior of these three sympatric species of Ips inhabiting Sitka spruce. Four objectives were proposed: (1) through field observations and laboratory studies determine the relative role of micro-habitat, emergence patterns, flight and brood development in providing species integrity among I. concinnus, I. t. tridens and I. plastographus; (2) to observe and document beetle behavior during initial pair formation in I. concinnus, I. t. tridens and I. plastographus in regard to eliminating or supporting the tactile aspect of pairing behavior as an isolating mechanism; (3) to describe the similarities and differences of the stridulatory apparatus for each sympatric species, including both sexes; and (4) to describe the acoustic signals and evaluate stridulation responses to various natural behavioral stimuli, comparing the acoustic responses inter- and intra-specifically. A general understanding of objectives one and two is necessary in evaluating the importance of objectives three and four, and are only supportive in this study.

## II. MATERIALS AND METHODS

### Biological Observations

To study field attack behavior, two Sitka spruce trees were felled on April 6 and one on May 23, 1975. Each was on a N-NW slope in a mixed stand of 150-year-old Tsuga heterophylla (Rafn.) Sarg. and Sitka spruce, 2.5 m north of Otis, Oregon in the Cascade Head Experimental Forest. Tree dimensions were 66-94 cm DBH and 27-37 m in length with a bark thickness range of 0.02-1.5 cm. A Foxboro Company hygrothermograph, measuring continuous daily temperature, was stationed at the study site from April through July 15.

Seven days after beetles were observed attacking trees in large numbers, four 30 cm-wide bark strips were removed from the circumference of the two trees felled April 6. One tree was divided into three equal sections and a bark strip removed at each section center; the other tree was sampled once at mid-bole. The scolytid galleries under the bark were mapped in relation to their lateral and horizontal position on the tree and proximity to other bark beetle galleries. Also, the number of female galleries per nuptial chamber was documented for I. concinnus and I. t. tridens.

On September 19, 1975 an 8 m infested log was obtained near Tillamook, Oregon, cut into 0.7 m sections, brought to Corvallis,

Oregon, and stored outside. On March 29, 1976 the log sections were placed in the greenhouse (temperatures ranging from 15.6°C to 27.8°C throughout the emergence period). Beetles were collected as they emerged, then identified to species, counted and sexed. During the emergence period, collections on eight days were separated into forenoon and afternoon periods. These days were April 2, April 4-8, April 13-14 and March 30-31, April 1-2, April 4-8 for I. t. tridens and I. concinnus, respectively. Sex of I. concinnus was confirmed by the presence, in males, of a larger median tubercle on the frons, spines on the elytral declivity that turn obliquely inward, and a longer, capitate third declivital spine (Lanier and Cameron, 1969). Because of difficulties in establishing accurate sexual dimorphisms, the genitalia were dissected for sex confirmation in I. t. tridens.

I. concinnus and I. t. tridens behavior, during initial gallery construction, was observed on fresh downed logs while beetles were actively climbing on the bark. Brood development was assessed by examining trees from the beginning of the 1975 spring flight through spring 1976. On each of seven examination days, 5-10 galleries were exposed per tree and the developmental stages (egg, larva, pupa and adult) noted. Comparison of daily study site temperature data with daily temperature recordings at the Cascade Head Experimental Forest weather station showed temperatures consistently 3°C lower at the study site. Thus, weather station temperatures were adjusted

for spring and summer by subtracting 3°C. From the adjusted temperature data a relative developmental rate for each stage was calculated using temperature-correlated immature development data from controlled laboratory studies on Blastophagus piniperda (L.) (Coleoptera: Scolytidae) in Norway (Bakke, 1968).

All beetles used in morphology and acoustic behavior studies came from naturally infested Sitka spruce collected near Otis or Tillamook, Oregon. Beetles necessary for acoustic behavior investigations were acquired as they emerged from naturally overwintered logs placed in the greenhouse, then sexed, placed in small, metal cans containing moist paper towel and stored (no longer than eight days) at 4°C until needed.

Quantitative and/or qualitative behavioral observations were made in conjunction with acoustic tape recordings during pair formation of I. concinnus, I. t. tridens and I. plastographus. From these observations of I. concinnus, a comparison of the relative time durations involved for each of five consecutive females to enter an attractive male nuptial chamber was possible. Additional observations of pairing behavior were observed in over 20 I. concinnus and nine I. t. tridens pairing situations. The gallery entering behavior in I. t. tridens and I. plastographus was not quantitatively analyzed because a full complement of females for the male could not be adequately replicated.

### Pars Stridens and Plectrum

Stridulatory apparatus measurements were taken from surgically removed stridulatory organs affixed to a microscope slide and viewed through a Bausch and Lomb compound light microscope fitted with a Filar Model 424C micrometer. Measurements on the stridulatory apparatus of 25 male and 25 female I. concinnus included total length, total width and ridge number of the pars stridens, while only length was recorded on the plectrum. Because the ridges on the pars stridens appeared denser cephalad, the structure was divided into two equal sections and counted. Using the SIPS computer program, individual headwidth measurements were plotted against the length of the pars stridens and number of ridges; and pars stridens length was regressed on the number of ridges for both sexes of I. concinnus. The plectrum of I. concinnus gradually tapers laterally, therefore measurement was recorded between the two points where tapering appeared to begin.

Because of availability, only five female I. plastographus stridulatory structures were measured according to their length, width and ridge number. Male I. plastographus and male and female I. t. tridens were examined with a compound light microscope to determine the presence or absence of stridulatory organs. All structures measured were oriented toward the observer in the same direction.

To compare intricate detail of the stridulatory structures or possible structures, electron micrographs were prepared for each species. Several methods were implemented in the scanning electron microscopy studies in order to adequately prepare and alleviate particulate contamination on specimens. Procedures included: critical point drying (Swaby, 1976, p. 13), which is particularly important to prepare the delicate pars stridens on female I. plastographus; application of Elmer's Glue to the stridulatory structure, allowing partial drying, with subsequent removal; and tandem washing with cellusole for 24 hours, xylene for 2 hours, then subjection to a 70% ethanol solution in an ultra-sonic vibrator for 10 minutes. A Mini-SEM Model MSM-2, using an accelerating potential of 15,000 kv, was used for scanning electron micrographs.

#### Acoustic Signals

A preliminary laboratory investigation was conducted on the pairing behavior of male and female I. concinnus and I. t. tridens to study the general timing of male nuptial chamber construction and subsequent male-female interactions as females join the growing polygamous family. In general, two questions appeared paramount: (1) at what point during nuptial chamber construction will the male permit entrance of a full complement of females without subsequent expulsion of any of those females and (2) what is the minimum time

interval necessary between introductions of consecutive females in an attractive male gallery? Information obtained in the preliminary investigations provided a timing basis for the acoustic tape recording studies. A minimum time interval between female introductions may be important in establishing the stimulus necessary to elicit a change in attraction chirps as females attempt entry. A change in attraction chirps may be expected in situations where: (1) the male exhibits different tactile and/or acoustic behavior; (2) there is a change in male and/or female pheromone milieu. These behavioral changes could be correlated with mean field attack sex ratios which may express relative female saturation levels for males.

Five I. concinnus males were introduced into preformed entrance tunnels in a fresh log, prevented from escape by placing a wire mesh screen over the tunnel opening and permitted to produce frass while constructing a nuptial chamber. Males were allowed to bore for 2.5 days at 24°C. Then, using soft forceps, one cooled (4°C) female was gently placed on the bark between two vertically oriented glass slides placed on their long edge, and allowed to walk 6 cm toward the male gallery opening. Subsequently, four additional females, each at 3 hour intervals, were allowed to attempt entry into each male gallery. As soon as a female approached the entry, acoustic and behavior responses were observed and monitored. A

tape recording was initiated as the female entered the hole and commenced stridulation.

Six chirps were sampled from each male and female pair through the fourth female accepted. Because only three males would accept the fifth female, ten chirps were sampled from the total produced in each replicate. Under identical pairing conditions, signals were tape recorded from beetles that were collected after they had re-emerged from an originally attacked log. Only when a male allowed the entrance of the third female were enough chirps produced to sample adequately. Ten chirps were randomly sampled from each of three replicates and compared statistically to the chirps emitted by fresh beetles.

Female I. concinnus that were subjected to the natural behavioral conditions of rivalry (several females placed together in a vacant male nuptial chamber) and hand-held stress (Michael and Rudinsky, 1972) did not stridulate. This led to use of an alternative, un-natural condition to ascertain if these beetles would stridulate under some type of stress so that comparisons to stridulations produced during the attraction context could be made. Four to eight females ( $n=2$ , 12 attempts made) were placed together in a 0.6 cm hole bored to 1.2 cm depth in fresh Sitka spruce, and the resultant sonic response was tape recorded. Thirty chirps, selected at random, were sampled from the total produced.

After four male I. concinnus had been allowed to bore for 2.5 days at 23°C, an intruder male was introduced into each male gallery, his escape prevented with an insect pin, and the acoustic response recorded. Thirty chirps were selected randomly and analyzed from the lumped replicate sum.

Four male I. t. tridens were introduced similarly to male I. concinnus, permitted to bore for two days at 24°C and (using the glass slide walls previously described for I. concinnus) four females two hours apart were allowed to enter the gallery of each male. A tape recording was made as females walked into the nuptial chamber. Stridulations were evaluated only qualitatively by oscillography.

Due to scarcity of I. plastographus beetles, preliminary studies could not be performed. Utilizing previous introduction methods two males were placed separately into the fresh bark of their host and left at 25°C for two days. A female was introduced into each attractive male gallery and the acoustic response tape recorded. Four females, placed between thumb and forefinger but allowing free head movement, were positioned 0.5 cm from the microphone and the stress stridulations recorded. After constructing a nuptial chamber for two days, three male I. plastographus were removed and three females per chamber were introduced and a tape recording was begun immediately. All chirps recorded in the attraction and rivalry

contexts were measured, whereas 30 chirps from the total were sampled in the hand-held stress situation.

Individual sound pressure pulses were counted and total duration of the combined pulses was measured for each chirp. From this information the pulse rate was calculated. If an interruption occurred within a chirp, pulse rate was based on total chirp duration minus interruption duration. Discrete gaps of silence within a chirp, termed interruptions, were produced in several behavioral conditions and prompted a quantitative comparison between species and behavioral context. Percentage of interrupted chirps per total sample, number of interruptions per interrupted chirp and mean duration of an interruption per chirp were calculated. Interruptions were operationally defined as having a distinct gap of silence not less than 4 ms in duration, and each subchirp possessing more than three sound pressure impulses. In addition to the above analysis, inter-species comparisons of stridulation pulse structure in the attraction context were made. Stridulations were oscillographed at increasing speeds for each species, such that individual internal pulse structure could be compared.

Tape recordings of attraction stridulations for each species were played back into a SAICOR Model 400 Spectrum Analyzer at original tape speed, and the frequency (kHz) was recorded.

Electronic sound equipment was used as described previously (Michael and Rudinsky, 1972) and included a Nagra 4.2 single track recorder exhibiting a flat frequency response from 0.22-22 kHz at a tape speed of 38 cm/second. A Hewlett-Packard Model 15119 A condenser microphone and a Princeton Applied Research Model 113 low noise preamplifier with bandwidth set at 0.3-100 kHz were used. Signal parameters were measured from sounds displayed on a Tektronix Model 5103N storage oscilloscope, and oscillograms were photographed with a Polaroid camera attached to the oscilloscope.

Sample comparisons for morphological and acoustic parameters were made in three ways: graphically, Student's t-test and analysis of variance. Calculations of 95% confidence intervals indicate significant differences ( $P < 0.05$ ) when intervals do not overlap, while samples in which the confidence interval of one sample includes the mean of the other are not considered significant (Simpson et al., 1960). Those situations intermediate between the two were subjected to Student's t-test. An analysis of variance ( $P < 0.05$ ) was used when equal sample sizes occurred within replicates. Confidence intervals and Student's t-test were calculated using equations in Snedecor and Cochran (1967) and analysis of variance was computed with the O.S.U. \*ANOVA 12 computer program.

### III. RESULTS

#### Biological Field Observations

I. concinnus and I. t. tridens inhabited the top side of the log along the full length of prostrate trees. Another bark beetle, Hylurgops rugipennis Mann., was abundant and was found predominantly in heavily shaded areas, characteristically exploiting the underside of the trees. Co-inhabitation of the host occurred frequently among attacking I. t. tridens and I. concinnus populations. I. plastographus was not observed on any tree examined during the experimental period.

Maximum emergence of I. t. tridens adults occurred several days behind I. concinnus when naturally overwintered logs were placed in the greenhouse (Table 1). The overall sex ratio indicated that females emerged in slightly greater numbers for I. concinnus whereas an equal number of each sex was present in the I. t. tridens population. The emergence data for I. concinnus do not indicate a definite sex ratio trend through time, but suggest that female emergence may be greatest in the first few days, males dominating sporadically on March 31 and then regularly from April 6-14. I. t. tridens males initially emerged in a higher proportion followed by increasing female emergence as time progressed. From the summed diel emergence data, the mean sex ratio (M:F) for

Table 1. Summary of results of Ips emergence from a Sitka spruce log placed in the greenhouse on March 29, 1976. Temperatures 15.6°C-27.8°C.

<u>I. concinnus</u>			<u>I. tridens tridens</u>		
Collection date	Number collected	Sex ratio (M:F)	Collection date	Number collected	Sex ratio (M:F)
March 29	20	1:1.50	March 29	0	-
30	49	1:1.58	30	1	-
31	32	1:0.60	31	0	-
April 1	102	1:1.27	April 1	11	1:0.38
2	63	1:1.17	2	72	1:0.53
3	32	1:1.29	3	231	1:0.42
4-5	43	1:1.15	4	723	1:0.78
6-14	32	1:0.52	5	309	1:0.94
			6	508	1:0.54
			7	754	1:1.15
			8	463	1:1.03
			9	228	1:1.05
			10	469	1:1.23
			11	248	1:1.41
			12-13	186	1:2.05
			14-21	215	1:2.26
Mean	373	1:1.14		4418	1:0.97

I. t. tridens during the morning period was 1:0.97 with a similar afternoon ratio of 1:1.03. I. concinnus showed a 1:1.02 and 1:1.07 sex ratio for the AM and PM periods, respectively.

Initial spring flight occurred at the experimental site on May 13, 1975 for I. concinnus, when a maximum daily temperature of 24°C was recorded. I. t. tridens was not found attacking observation logs at this time. A period of cool days followed and there was mass flight and attack of both species between May 30 and June 6 when temperatures became favorable for flight. Males of both species constructed galleries under or along the outer edge of bark flakes and in bark fissures. Males bored through the outer bark, approximate to or on the bark-xylem interface, constructed a nuptial chamber and subsequently allowed a characteristic number of females to enter the nuptial chamber: I. concinnus, 1-5 females ( $\bar{x} = 2.3 \pm 0.19$ ; n=89) and I. t. tridens, 2-8 females ( $\bar{x} = 3.7 \pm 0.45$ ; n=43). I. t. tridens females excavated their egg galleries approximately parallel to the wood grain, and deposited eggs singly in niches carved along each side of the gallery. According to Bright and Stark (1973), the number and frequency of eggs deposited is apparently correlated with moisture and nutritional factors of the host. Gallery construction in I. concinnus was different, with the female excavating a short, crescent-shaped egg gallery in which 2-5 eggs were deposited in pockets constructed on the outer gallery edge.

I. concinnus and I. t. tridens developed concurrently and each completed one generation per year (Fig. 1). Beetles attacking in the spring completed their development by fall and overwintered as adults. Adults colonizing in July (May 23 tree) reached the larval stage by late fall and overwintered as larvae or continued development at a reduced rate. Most adults of these two species overwintered under the bark of their originally colonized tree. However, heavily infested logs which were monitored throughout the season in 1974 showed that few adults were present in January 1975, indicating that adults also spent the winter outside brood logs, presumably in the forest litter. In summary, both species attacked their host from May through late summer or early fall; a portion of the originally attacking adults re-emerge after egg hatch; and each species appears to have a life cycle consisting of a single generation with overlapping broods.

#### Pairing Behavior

Upon coming in contact with male frass near the entrance tunnel, female I. concinnus exhibited attraction behavior similar to female I. paraconfusus (Barr, 1969), I. calligraphus (Wilkinson et al., 1967) and I. pini (Swaby, 1976). With legs moving rapidly in digging motions, and head and antennae down, the females moved through the frass until they reached the gallery opening where they

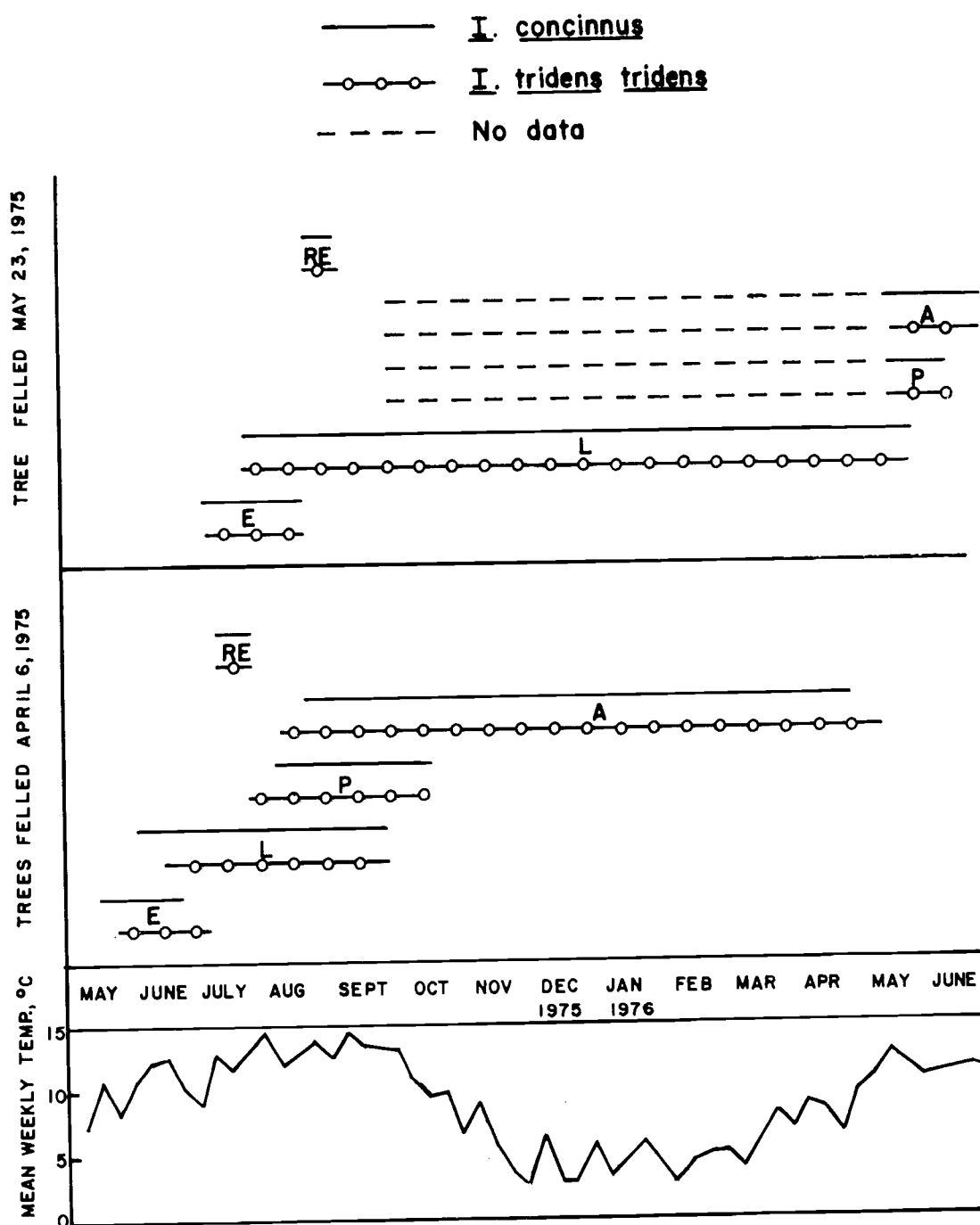


Fig. 1. Development of Ips concinnus and Ips tridens tridens near Otis, Oregon. E = egg; L = larva; P = pupa; A = adult; RE = re-emergence of adults.

immediately began descending toward the nuptial chamber. Stridulation was audible only after the female entered the entrance tunnel and tactile contact with the male had presumably occurred. Stridulation was most prominent during initial pairing formation but subsequently decreased, and eventually ceased, when the female entered the nuptial chamber. Acoustic output was usually associated with a forward and backward movement of the female as she contacted the male while progressing down the entry gallery. When this behavior ceased, acoustic signals also decreased or ended.

During acceptance of the first three females, males were not observed near the top of the entrance and females disappeared within 0.5-3.5 minutes after entering the gallery opening. However, the fourth and fifth females generally experienced greater resistance from the male, and females typically stridulated more energetically and spent more time moving forward and backward while slowly descending into the nuptial chamber. Males pushed the female with their elytral declivity during resisting behavior. Females in this situation took from two minutes to three hours ( $\bar{x}$  = 46 minutes) to disappear from view, and in two of five cases, males were at the gallery opening and prevented entrance of the fifth female. Males excluding females exhibited very vigorous backward motions, which lasted only a few seconds before the female quickly retreated from the entrance tunnel.

Female I. t. tridens and I. plastographus behaved comparably to female I. concinnus when exposed to their specific male frass in proximity to the entrance tunnel. Behavior of male I. t. tridens differed slightly from male I. concinnus because of the habit of immediately positioning his elytral declivity flush with the entrance as any attracted female began to move into the tunnel. I. t. tridens females were repelled from the gallery by the male's discrete, vigorous thrust to the head of the attracted female. During female acceptance the pair moved slowly down the gallery entrance and exhibited forward and backward movements. From the few observations, it appeared that more time was required for female acceptance as the number of females per nuptial chamber increased. Documentation of pairing behavior during male acceptance of several consecutive females was not possible for I. plastographus. However, the behavior of the male accepting the first female suggests that no basic difference exists between I. plastographus and the other two sympatric species.

#### Stridulatory Apparatus

##### Ips concinnus

Male and female I. concinnus possess a gular-prosternum stridulatory apparatus (Barr, 1969) with the pars stridens (file)

located medially on the "gula" of the head and consisting of a transverse series of ridges in two sections separated by the median suture (Fig. 2A, D). The ridges of the pars stridens are typically broadly rounded and branched or unbranched as they extend across the gula (Fig. 2B, E). The plectrum (scraper) is a single transverse ridge of integument directly dorsal and median to the anterior edge of the prosternum (Fig. 2C, F).

Descriptive morphological data are presented and statistically compared in Table 2. The female pars stridens contains a mean of 106 ridges and is shorter ( $P < 0.05$ ) with fewer ridges ( $P < 0.01$ ) when compared to the male pars stridens. Ridges on the male pars stridens are somewhat wider apart than the female and the ratio of ridges to total file length (ridges/mm) is also lower in the male. In each sex the ridges become more dense in the anterior half of the pars stridens ( $P < 0.05$ ). Total width of the pars stridens was  $0.17 \text{ mm} \pm 0.011$  for males and  $0.19 \text{ mm} \pm 0.01$  for females. Plectrum length was significantly longer in females ( $P < 0.05$ ).

Male and female head width was positively correlated with file length and number of ridges per file (Table 3).

#### Ips tridens tridens

Barr (1969) reported that this species lacked stridulation organs and was thought to be silent. However, I found that this species

Fig. 2. Scanning electron micrographs of the stridulatory apparatus of I. concinnus. Pars stridens on the head: female (A) 400X, (B) 2000X; male (D) 400X, (E) 2000X. Plectrum on the prosternum: female (C) 100X; male (F) 100X. Arrow designates plectral ridge and CX = coxa. All micrographs are oriented with the anterior toward the top.

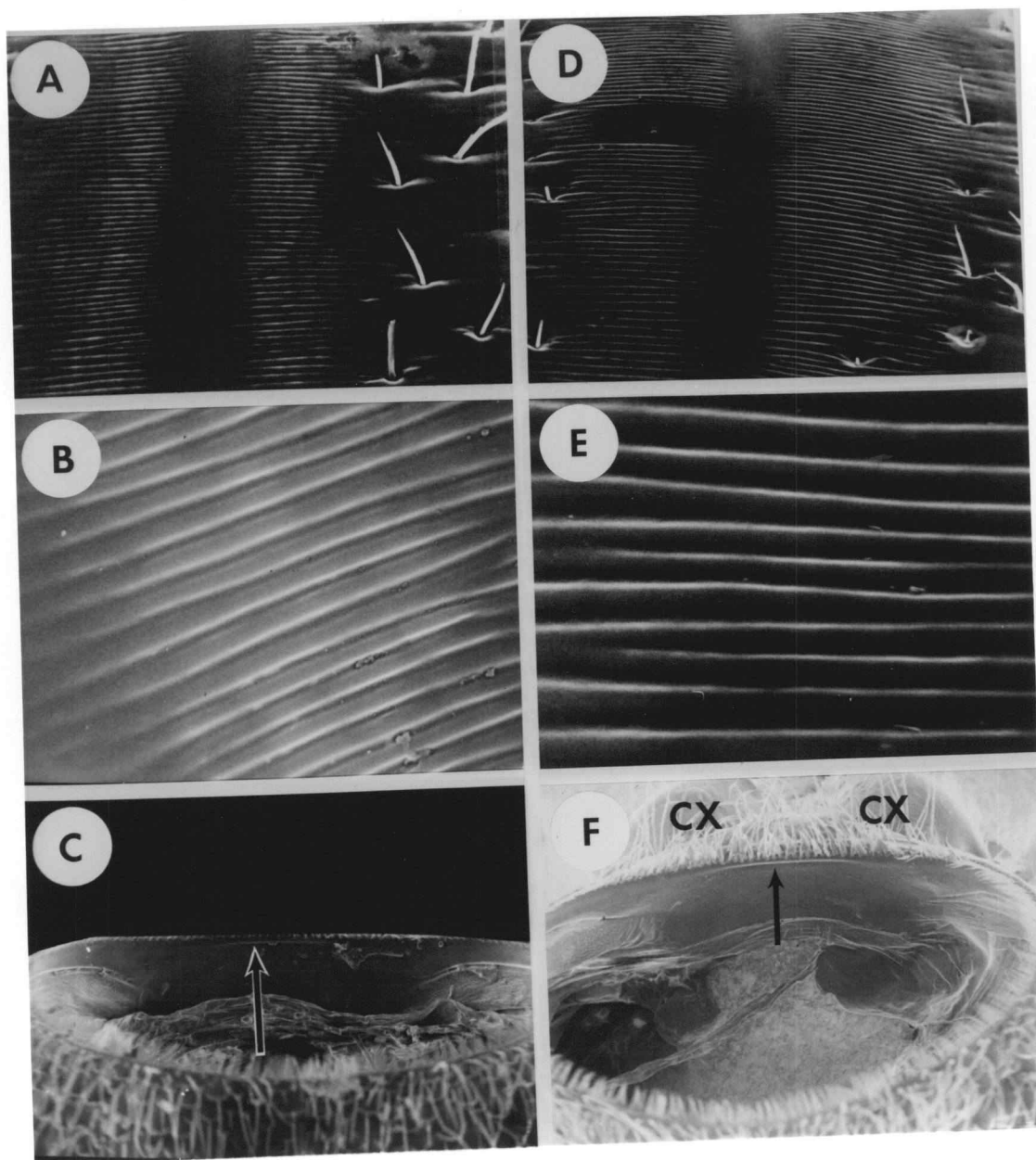


Table 2. Measurements of the stridulatory apparatus on Ips concinnus.<sup>1</sup>

Parameter measured	Female			Male		
	Mean	Range	95% Confidence interval	Mean	Range	95% Confidence interval
Head width (mm)	1.19	1.05-1.31	1.16-1.22*	1.23	1.11-1.32	1.21-1.26*
File length (mm)	0.39	0.34-0.46	0.37-0.40*	0.42	0.39-0.47	0.41-0.43*
No. ridges on file:						
anterior half	59	49-69	57-61**	63	58-75	61-64**
posterior half	45	41-52	44-47**	49	42-59	47-50**
total	106	92-121	103-108***	111	102-134	109-114***
Distance between ridges (μ):						
anterior half	3.24	2.82-3.62	3.15-3.34**	3.36	3.15-3.51	3.32-3.49**
posterior half	4.23	3.58-4.73	4.12-4.35**	4.32	3.36-5.02	4.19-4.45**
total	3.65	3.18-4.01	3.56-3.74*	3.78	3.52-4.05	3.72-3.84*
Ratio: no. ridges to file length (ridges/mm)	275	250-303	268-281*	266	247-284	262-270*
Plectrum length (mm)	0.37	0.29-0.48	0.35-0.39*	0.32	0.23-0.44	0.30-0.34*

\*Indicates significant difference at  $P < 0.05$  in same horizontal line.

\*\*Indicates significant difference at  $P < 0.05$  in same vertical column.

\*\*\*Indicates significant difference at  $P < 0.01$  in same horizontal line.

<sup>1</sup>  
n = 25

Table 3. Regression of file length and the number of ridges on head width, and the number of file ridges on file length of male and female Ips concinnus.<sup>1</sup>

y	Male		Female	
	Equation	R	Equation	R
File length	$y = 0.048 + 0.302 \text{ (head width)}$	0.6956**	$y = 0.01 + 0.315 \text{ (head width)}$	0.7294**
No. ridges	$y = 43.9 + 54.7 \text{ (head width)}$	0.4559*	$y = 32.2 + 61.4 \text{ (head width)}$	0.6548**
No. ridges	$y = 20.8 + 215.5 \text{ (file length)}$	0.7802**	$y = 42.2 + 16.4 \text{ (file length)}$	0.7557**

\*Regression significant at  $P < 0.05$ .

\*\*Regression significant at  $P < 0.01$ .

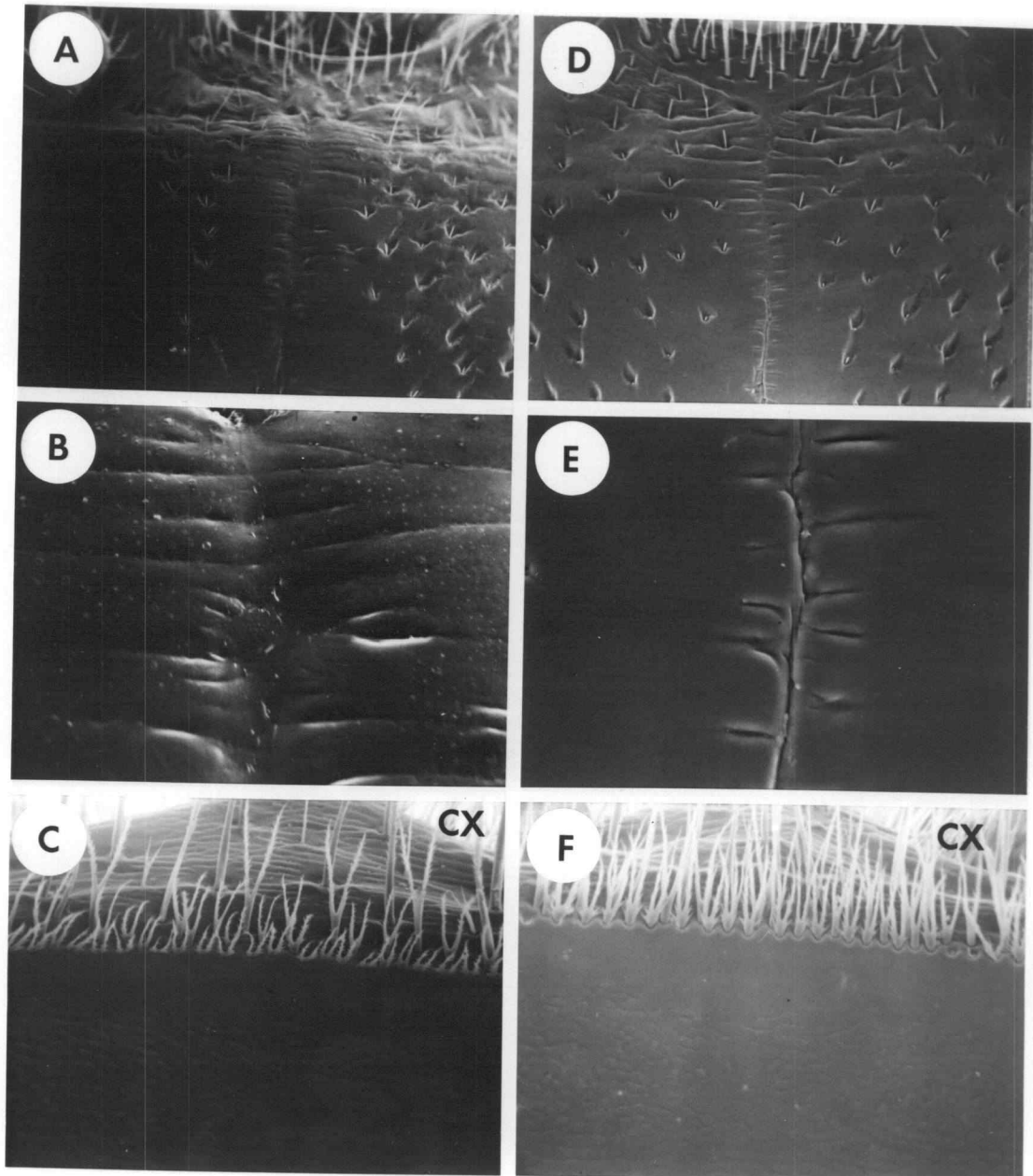
<sup>1</sup><sub>n</sub> = 25

produced brief clicks, although a stridulatory apparatus could not be identified or located (Oester and Rudinsky, 1975). Electron micrographs of male and female I. t. tridens which depicted the gular and prosternum regions analogous to stridulatory apparatus regions on I. concinnus, revealed several rudimentary transverse ridges on the gula, but no specialized scraping structure on the prosternum (Fig. 3C, F). Observations of female behavior during her entrance into the male gallery did not reveal a stridulatory mechanism. I was unsuccessful in detecting any stridulatory organs in the vertex-pronotal regions or various other alternate areas on the beetle, using a compound light microscope.

#### Ips plastographus

Female I. plastographus possess a vertex-pronotal-type stridulatory organ, first reported by Barr (1969). A detailed description of this stridulatory organ is given by Barr (1969). One of the two organs involved in stridulation is on the median vertex of the head near the occipital region, and the other is on the underside of the pronotum, near the anterior edge. Both consist of a closely spaced series of parallel transverse ridges tapering at both poles and conceivably capable of vibration. In the literature the term *pars stridens* is consistently associated with the organ on the head while the ridges on the pronotum have been termed the *plectrum* (Barr,

Fig. 3. Scanning electron micrographs of the gula and anterior edge of the prosternum of male and female Ips tridens tridens. Gular region: male (A) 400X, (B) 1000X; female (D) 400X, (E) 1000X. Anterior prosternum region: male (C) 400X; female (F) 400X. CX = coxa. All micrographs oriented with the anterior toward top.



1969). In this species the pars stridens is a raised elongated structure with short, rounded, unbranched ridges (Fig. 4A, B, C), that includes three times more ridges ( $P < 0.05$ ) than the 80 ridges found on the plectrum (Table 4). The convex, oval-shaped plectrum is a differentiation of the membrane on the underside of the pronotum (Fig. 4D, E, F). Its rounded ridges frequently are branched and are spaced a four-fold greater distance apart ( $3.98 \mu$ ) with a much lower ratio of ridges to total file length (253/mm) when compared to the pars stridens ( $1.04 \mu$  and 964/mm respectively) (Table 4). The space between plectrum and integument in this species may have a resonance function similar to that suggested by Barr (1969). From the descriptive data and SEM micrographs the pars stridens appears longer and narrower than the plectrum. Using light microscopy, no obvious specialized stridulatory structures were found on the male in either the gular-prosternum or vertex-pronotum regions of the beetle. A trough is present on the vertex of the male, but lacks ridges. However, vestigial structures similar to those found on male and female I. t. tridens occur on the median area of the gula of male and female I. plastographus.

Stridulation is produced when the female beetle withdraws her head partially into the pronotum, engaging the two organs and stroking forward or backward in one continuous movement. Although beetle movement during sound production was not observed in this

Fig. 4. Scanning electron micrographs illustrating the stridulatory organs of female Ips plastographus. Pars stridens: overall view on the vertex of head (A) 50X, (B) 700X; detailed view of ridges (C) 5000X. Plectrum: overall view on the underside of pronotum (D) 100X, (E) 400X; detailed view of ridges (F) 1000X.

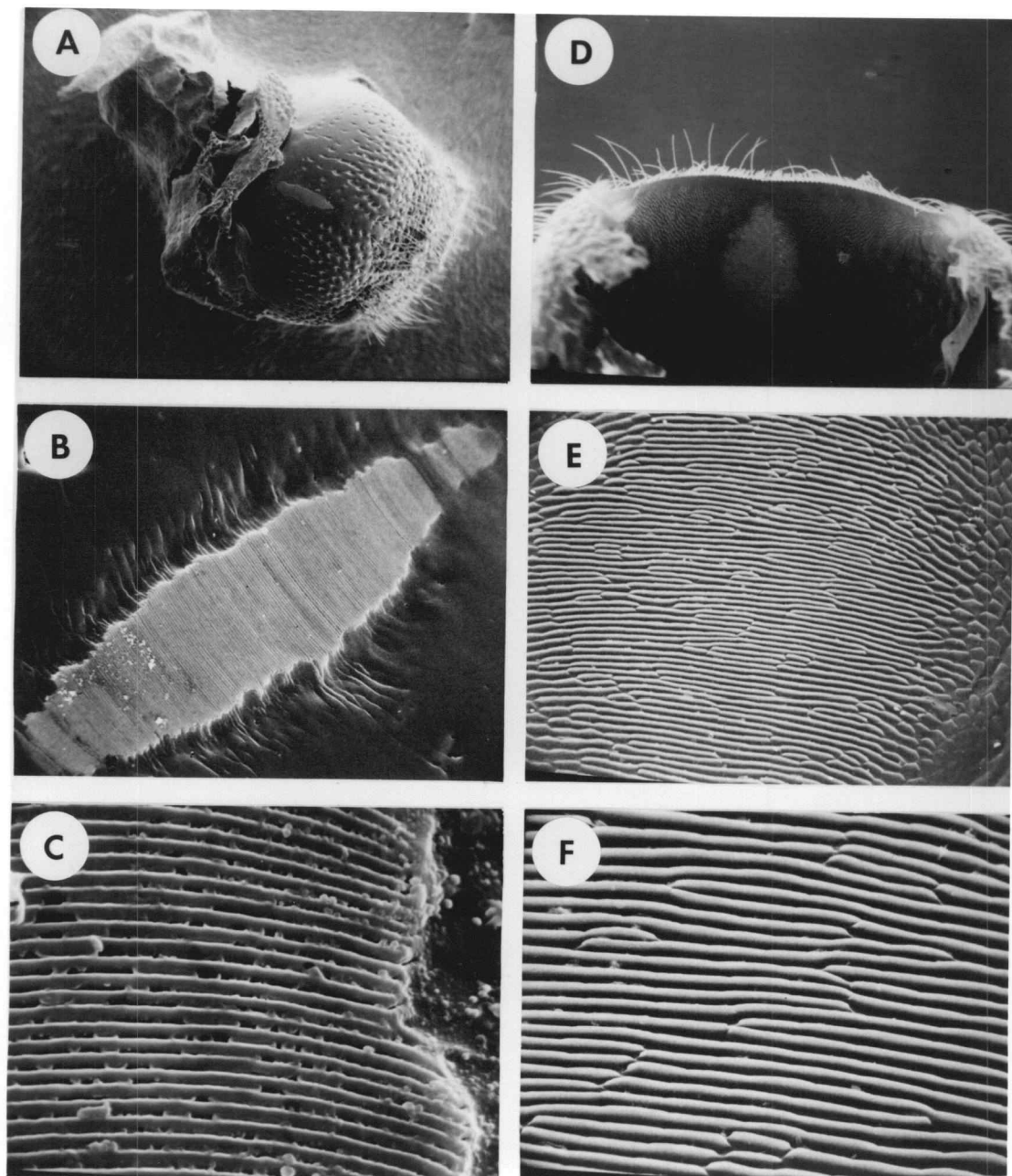


Table 4. Measurements of female Ips plastographus vertex-pronotum stridulatory apparatus.<sup>1</sup>

Parameter measured	Pars stridens			Plectrum		
	Mean	Range	95% Confidence interval	Mean	Range	95% Confidence interval
Head width (mm)	1.02	1.01-1.14	0.93-1.12			
Pronotum length (mm)				1.63	1.51-1.76	1.50-1.75
Length (mm)	0.27	0.22-0.30	0.22-0.31	0.32	0.29-0.38	0.27-0.37
Width (mm)	0.06	0.05-0.08	0.05-0.07	0.24	0.21-0.27	0.21-0.27
Number of ridges	255.00	216-276	226-285	80.00	72-97	68-93
Distance between ridges ( $\mu$ )	1.04	0.96-1.10	0.96-1.11	3.98	3.65-4.54	3.53-4.44
Ratio of no. of ridges to length (ridges/mm)	964	923-1040	897-1032	253	220-274	225-280

<sup>1</sup><sub>n</sub> = 5

species, Wilkinson et al. (1967) reported stridulation was produced principally during the backward movement of the vertex of the head in I. calligraphus, which has a similar stridulatory apparatus.

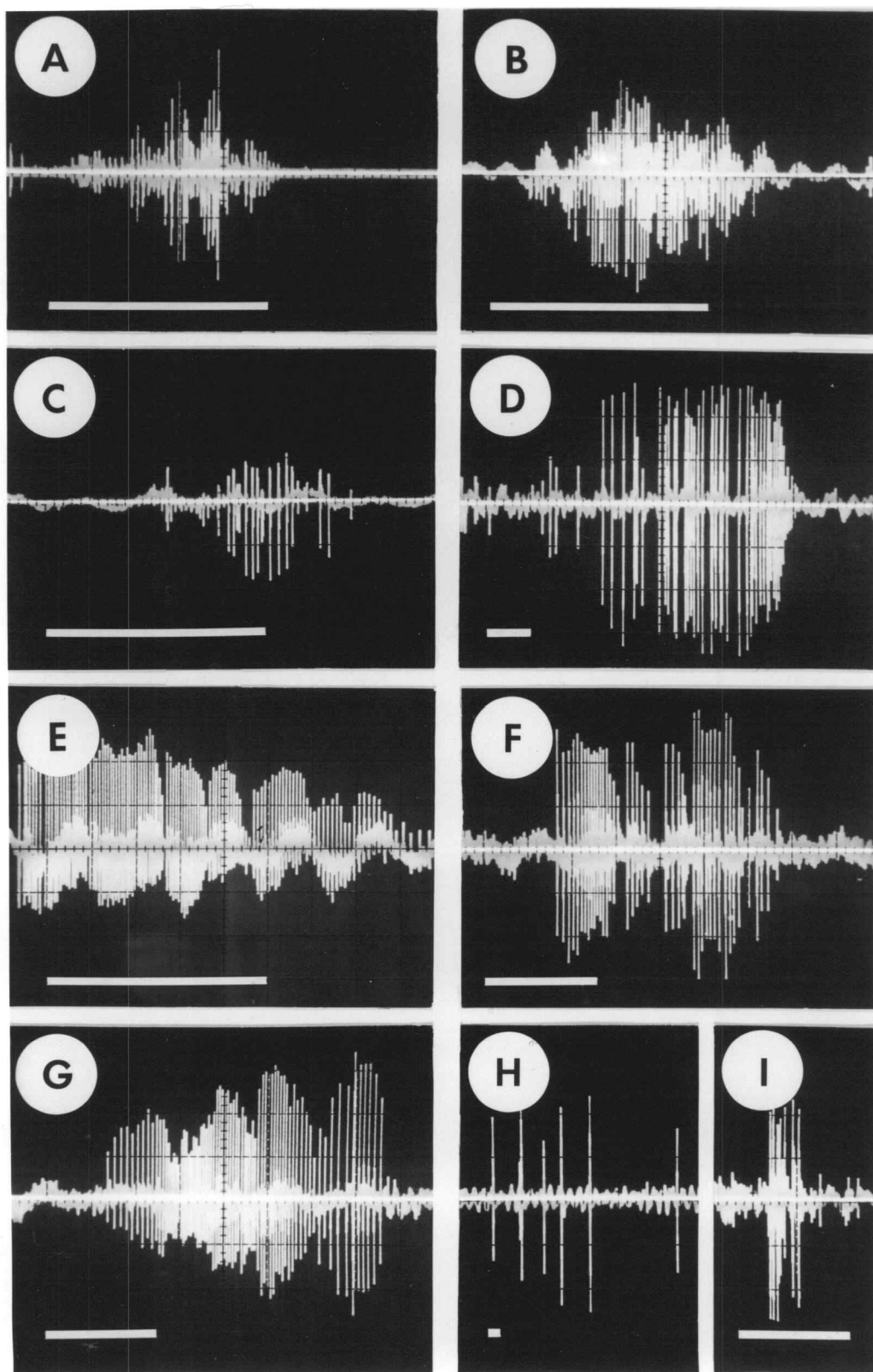
### Signals

#### Ips concinnus

Oscillograms of chirps selected to illustrate mean parameter measurements of I. concinnus, in several behavioral contexts, are shown in Figure 5A-D. A chirp is defined as a sound that is perceived as unitary to the human observer's ear (Broughton, 1963). Chirps in this species consisted of a series of sound pressure impulses characteristic of the multi-impulse signals recorded in other acoustic studies of Scolytidae (Wilkinson et al., 1967; Michael and Rudinsky, 1972; Swaby and Rudinsky, 1976).

Statistical analyses of stridulations produced in the various behavioral contexts indicated several differences within the acoustical parameters measured. The fact that male and female I. concinnus have similar stridulations prevented distinguishing attraction chirps as male or female. For each consecutive female that the male accepted there was an increase in all mean stridulation parameters up to the fifth female, when the parameter value decreased slightly (Fig. 6-8). Attraction chirps were highly variable; e.g. pulse number per chirp ranged from 16 to 104 (Fig. 6). The variation among

Fig. 5. Oscillographs illustrating parameter means of stridulations produced by Ips. Ips concinnus: Male plus female-1 attraction chirp (A), 25°C; male plus female-3 attraction chirp (B), 25°C; female stress chirp (C), 27°C; male aggression chirp (D), 25°C. Ips plastographus: female attraction chirp (E), 26°C; female rivalry chirp (F), 26°C; female stress chirp (G), 26°C. Ips tridens tridens: attraction click (H) and chirp (I), 28°C. Each bar = 50 milliseconds.



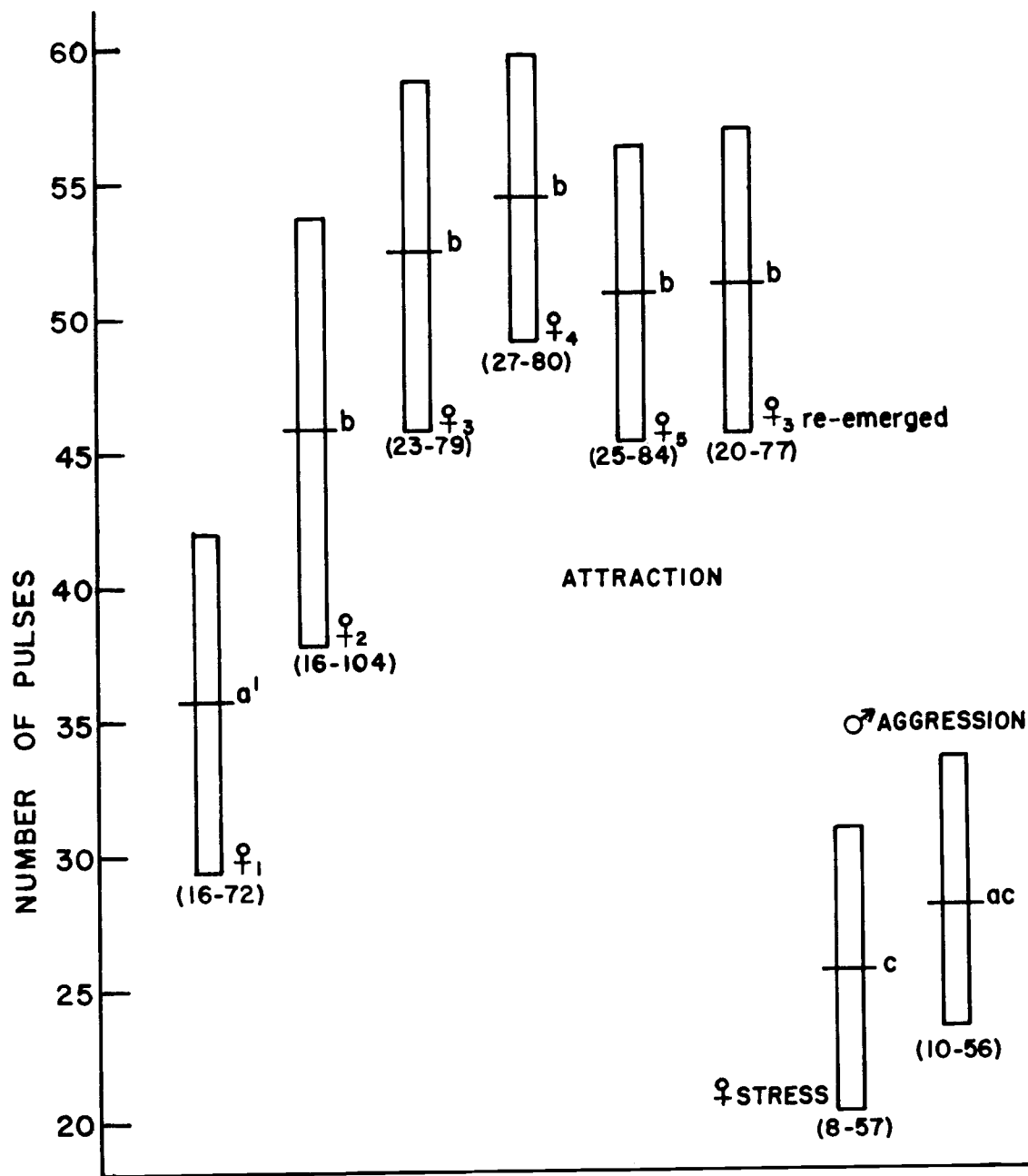


Fig. 6. Mean and 95% confidence intervals of pulse number per chirp in several behavioral categories for *Ips concinnus*. Bracketed numbers indicate range.

<sup>1</sup> Different letters indicate significant differences at  $P < 0.05$ .

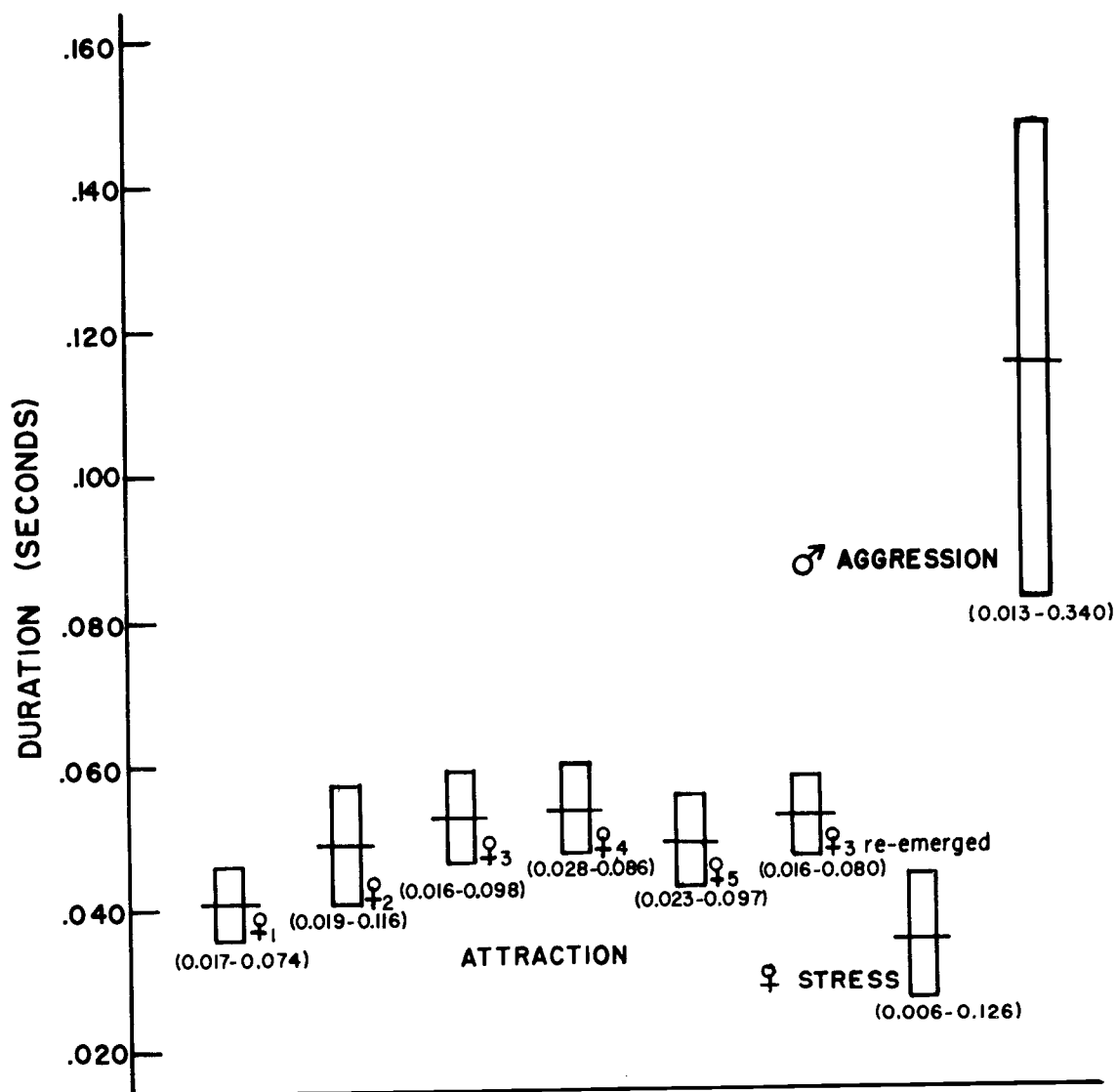


Fig. 7. Mean and 95% confidence intervals of chirp duration in several behavioral categories for *Ips concinnus*. Bracketed numbers indicate range.

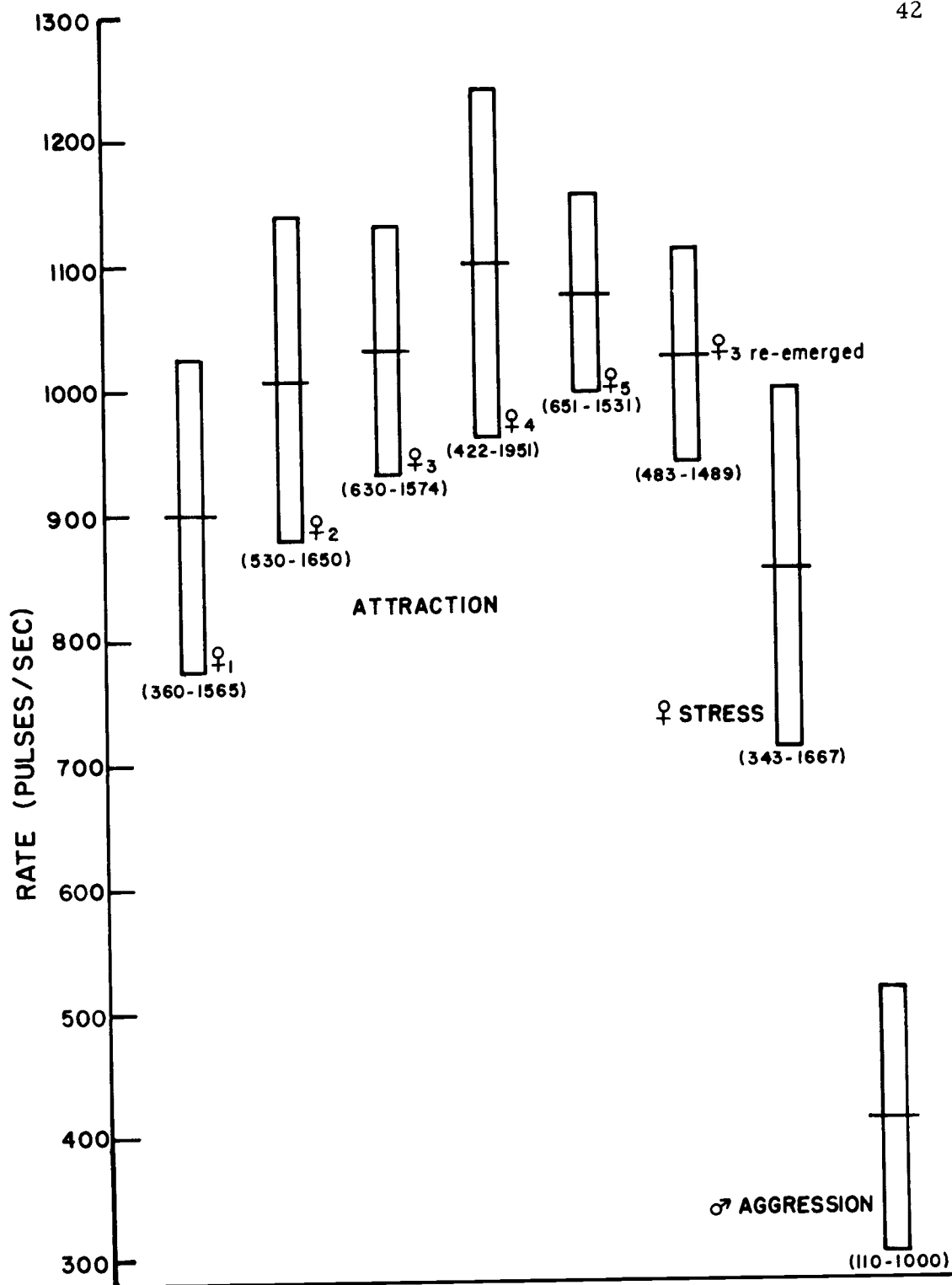


Fig. 8. Mean and 95% confidence intervals of pulse rate per chirp in several behavioral contexts for *Ips concinnus*. Bracketed numbers indicate range.

means was not as great; stridulations recorded as a male was accepting the first female had a mean of 36 pulses, whereas the fourth female to join stimulated production of chirps having a mean of 54 pulses per chirp (Fig. 5A, B; 6). Chirps emitted during pairing of the first female had statistically fewer pulses per chirp than those produced when the second, third, fourth and fifth females were entering ( $P < 0.05$ ). In contrast, measurements of chirp duration showed that only signals produced when the third female entered an attractive male gallery were longer than those emitted as the first female descended ( $P < 0.05$ ) (Fig. 7). A faster pulse rate occurred in chirps produced as the third ( $P < 0.01$ ) and fifth ( $P < 0.05$ ) female paired with the male when compared to the first female; all other combinations were similar (Fig. 8).

Although interrupted chirps occurred intermittently, no difference was apparent in the number of interrupted chirps or duration of a single interruption per chirp in any of the I. concinnus behavioral contexts (Table 5). Relative frequency of a stridulation emitted during attraction behavior ranged from 1.5-13 kHz with major energy bands occurring between 4-13 kHz (Fig. 9). Oscillographic analysis of an attraction chirp at decreasing chirp speeds indicated that individual pulses consisted of several spikes which decay to the start of the following pulse (Fig. 10A, B, C).

Table 5. Interruption data for chirps of Ips concinnus and Ips plastographus.

Species and behavioral context	n	Percent interrupted chirps	Number of interruptions per interrupted chirp	Average duration of single interruption (sec.)
<u>I. concinnus</u>				
attraction	150	13	1.6	0.0033
♀ stress	30	17	1.4	0.0043
♂ aggression	30	37	1.7	0.0163
<u>I. plastographus</u>				
♀ attraction	22	17	2.3	0.0088
♀ stress	30	27	2.4	0.0104
♀ rivalry	30	72	2.7	0.0190

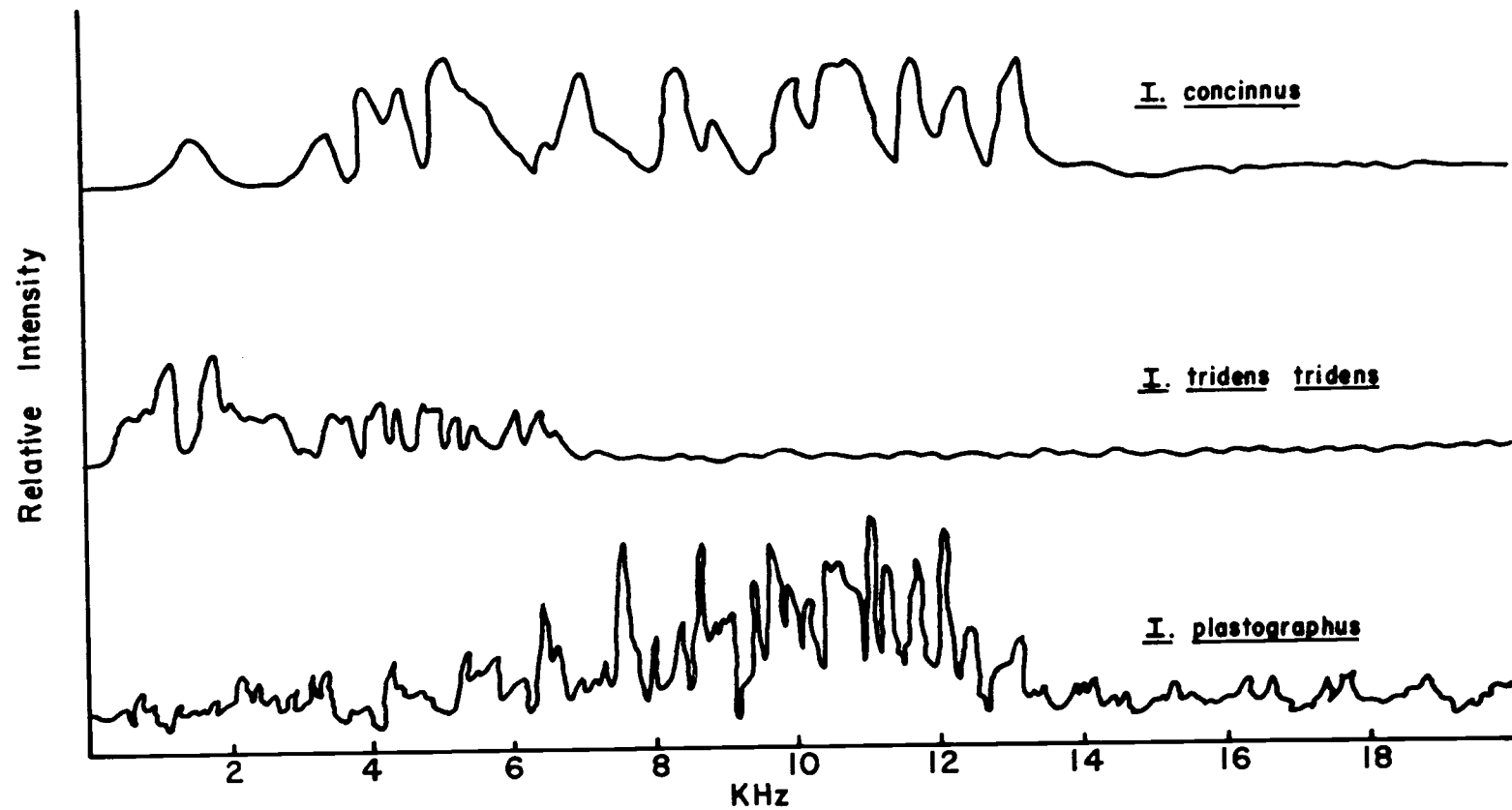
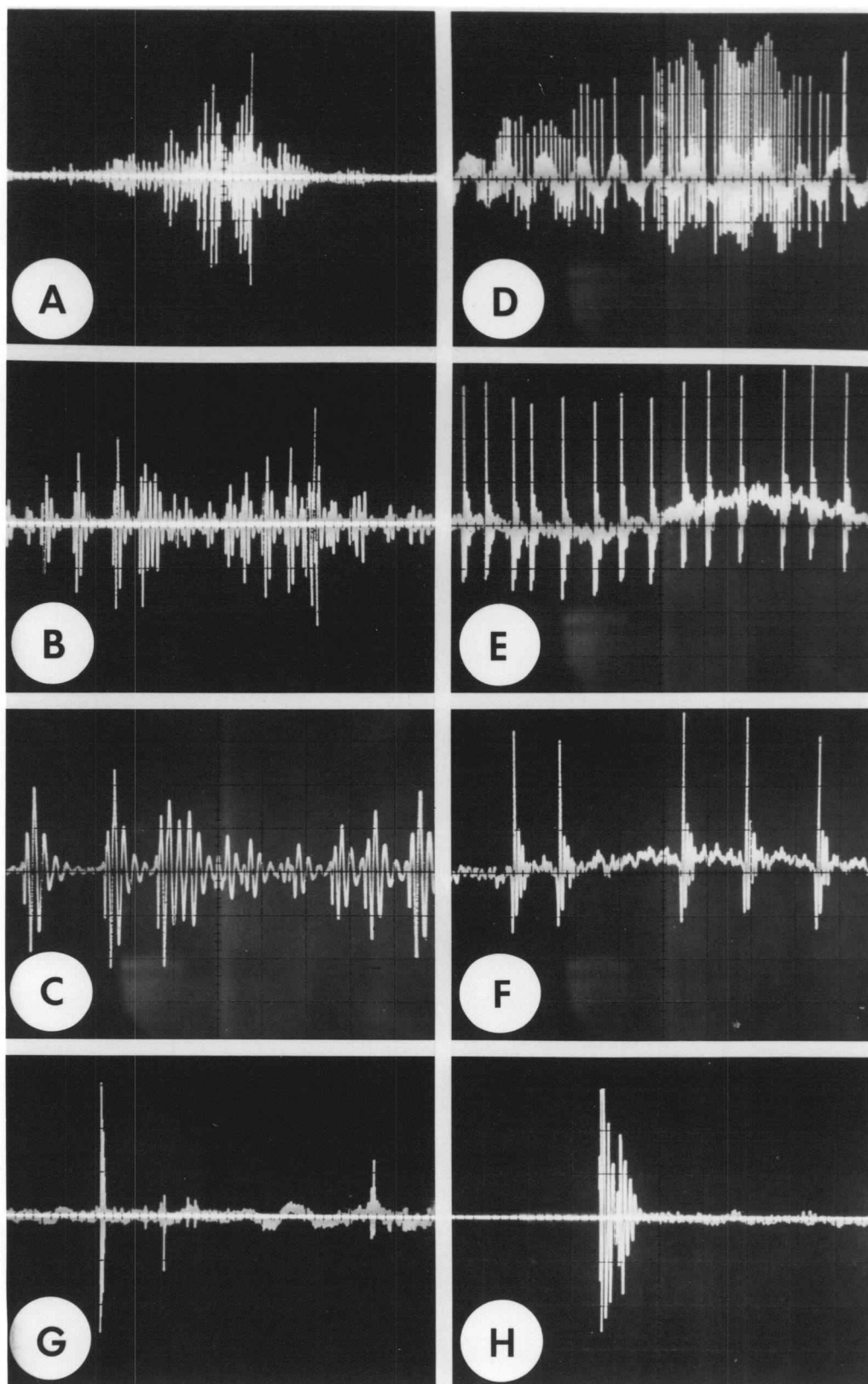


Fig. 9. Audio spectrum graphs of attraction stridulations of Ips concinnus, Ips plastographus and Ips tridens tridens.

Fig. 10. Oscillographs depicting chirp and click structure of Ips. Female attraction chirp of Ips concinnus: abscissa time scale A) .02 sec., B) .005 sec., C) .002 sec. Female attraction chirp of Ips plastographus: D) .02 sec., E) .005 sec., F) .002 sec. Attraction click (sex unknown) of Ips tridens tridens: G) .005 sec., H) .002 sec.



Females subjected to crowding produced acoustic responses (stress chirps) similar in structure to attraction chirps (Fig. 5C). Individual stridulations contained a mean of 25 pulses, which was significantly fewer ( $P < 0.05$ ) than attraction chirps (Fig. 6). Stress acoustic responses were shorter in duration ( $P < 0.05$ ) and slower in pulse rate ( $P < 0.05$ ) when compared to female 2-5 and 3-5 attraction stridulations respectively (Fig. 7, 8).

Male I. concinnus produced acoustic signals when subjected to a behavioral condition evoking fighting (Fig. 5D). The behavior was as follows: the male rapidly pushed the intruder male backward until the intruder came in contact with the insect pin blocking the entry or was rejected from the gallery. Stridulation was intermixed with scratching noises from apparent tactile contact (Oester and Rudinsky, 1975), but it was not established which male was stridulating. Although a general oscillograph of male stridulation was shown by Oester and Rudinsky (1975), Figure 5D illustrates the statistical means of the three parameters measured for better visual comparisons. Aggressive acoustic responses consisted of fewer pulses per chirp than stridulations produced as females 2-5 entered an attractive male gallery ( $P < 0.05$ ) (Fig. 6). Additionally, male chirps were longer in duration ( $P < 0.05$ ), had a slower pulse rate ( $P < 0.05$ ) and slightly more interruptions than chirps produced in the attractive or female stress categories (Fig. 7, 8; Table 5).

Ips tridens tridens

Sonic response was detected and recorded as the male and female came together during initial pair formation. The sounds produced appeared as brief, multi-impulse "clicks" (Broughton, 1963) and occurred singly (Fig. 5H), serially without pattern, or serially and structurally resembling a distended chirp (Fig. 5I). The criteria for designating whether a sound was a click or a scratch was based on the uniformity of the individual sound pressure impulses when viewed oscillographically. Scratching sounds consisted of several sound pressure spikes that were irregularly spaced and jagged in appearance, whereas the spikes within a click were evenly spaced and symmetrical (Fig. 6H). Female clicks recorded under conditions of artificial stress and male clicks recorded during aggressive behavior consisted of several sound pressure impulses and appeared similar to the single attraction clicks (Oester and Rudinsky, 1975). Male behavior in the aggressive context was similar to that reported for I. concinnus above. The distended attraction sounds produced by I. t. tridens are not phonically comparable to chirps produced by either sex of I. concinnus or female I. plastographus. Instead, they are similar to a "rasp," quite unlike the higher pitched, definite chirp of the other two species. Although these sounds are chirp-like, it should not be discounted that they may have resulted from tactile

interactions. It is not inconceivable that the female could scrape parts of her head or mandibles on the male declivity and create such a sound. The unconforming variability of stridulations, in combination with intermittent scratching by the interacting beetles during pair formation, presented difficulties in sampling and prevented a comparative statistical evaluation.

Relative frequency of the extended chirp-like stridulations was in the range of 1-6.5 kHz (Fig. 9). Each click consisted of several sound pressure spikes (Fig. 10G, H).

#### Ips plastographus

Under the described conditions of attraction, stress and rivalry, I. plastographus females produced stridulations consisting of many sound pressure impulses, structurally similar to I. concinnus male and female chirps and other Scolytidae (Wilkinson et al., 1967; Michael and Rudinsky, 1972; Swaby and Rudinsky, 1976). Pulse number per chirp was not different between behavioral contexts, with means ranging from 56 to 80 (Table 6). Although chirp duration was not statistically different ( $P < 0.05$ ), pulse rate within attraction chirps was faster than stress ( $P < 0.05$ ) or rivalry ( $P < 0.05$ ) (Table 6). Interestingly, rivalry stridulations were characterized by a much higher percentage of interrupted chirps per sample and by a doubling of the mean duration per single interruption within a chirp,

Table 6. Chirp parameters of female Ips plastographus in the behavioral situations of attraction, stress and rivalry.

Behavioral context	n	Pulses per chirp			Duration (sec)			Pulse rate (pulses/sec)		
		range	$\bar{x}$	95% confidence interval	range	$\bar{x}$	95% confidence interval	range	$\bar{x}$	95% confidence interval
Attraction	22	31-148	76	65-98a <sup>1</sup>	0.030-0.195	0.108	0.080-0.136a	333-1684	890	711-1068a
Stress	30	20-166	80	62-97a	0.042-0.270	0.134	0.105-0.163a	333-1368	639	542-737b
Rivalry	30	6-160	57	40-73a	0.024-0.525	0.148	0.099-0.196a	204-1485	578	436-720b

<sup>1</sup> Different letters indicate significant differences at  $P < 0.05$  in same vertical column.

when compared to chirps in the stress or attraction context (Table 5).

In the rivalry behavioral context, an atypical stridulation was detected four times. These chirps possessed mean acoustic parameters of: a) 212 pulses per chirp; b) 0.344 seconds duration; and c) a rate of 721 pulses/second. The number of pulses per chirp was four times greater than the mean and 52 pulses more than the highest recorded in the rivalry sample (Table 6). It is not known if these anomalous stridulations represent a real, but rare, signal, or are incidental.

Audiospectrographic analysis indicated relative frequencies of an attraction stridulation in the range of 6.5-12.5 kHz (Fig. 9). Single pulse structure within attraction chirps was uniform and had relatively few spikes which decayed very quickly into the next pulse (Fig. 10 D, E, F).

#### Stridulation Differences between Species

The erratic acoustic signals produced by I. t. tridens in the attraction context differed in frequency, duration, pulse rate, number of pulses per chirp and general envelope structure when compared to I. concinnus and I. plastographus. Although pulse rate and frequency were somewhat similar between I. concinnus and I. plastographus, the number of pulses and chirp duration per chirp appeared different.

From 95% confidence interval calculations attractive stridulations of I. plastographus were composed of 63 to 90 pulses and had a length of 0.08 to 0.135 second, while I. concinnus chirps in all male-plus-female situations consisted of 29 to 60 pulses and were 0.036 to 0.06 second in duration (Fig. 11). Both of these parameters were significantly different ( $P < 0.05$ ) with no overlapping confidence intervals between species. Pulse duration within chirps or clicks also appeared different between these species. The three species ranked in order of decreasing individual pulse duration and spike content are: (1) I. t. tridens; (2) I. concinnus; (3) I. plastographus.

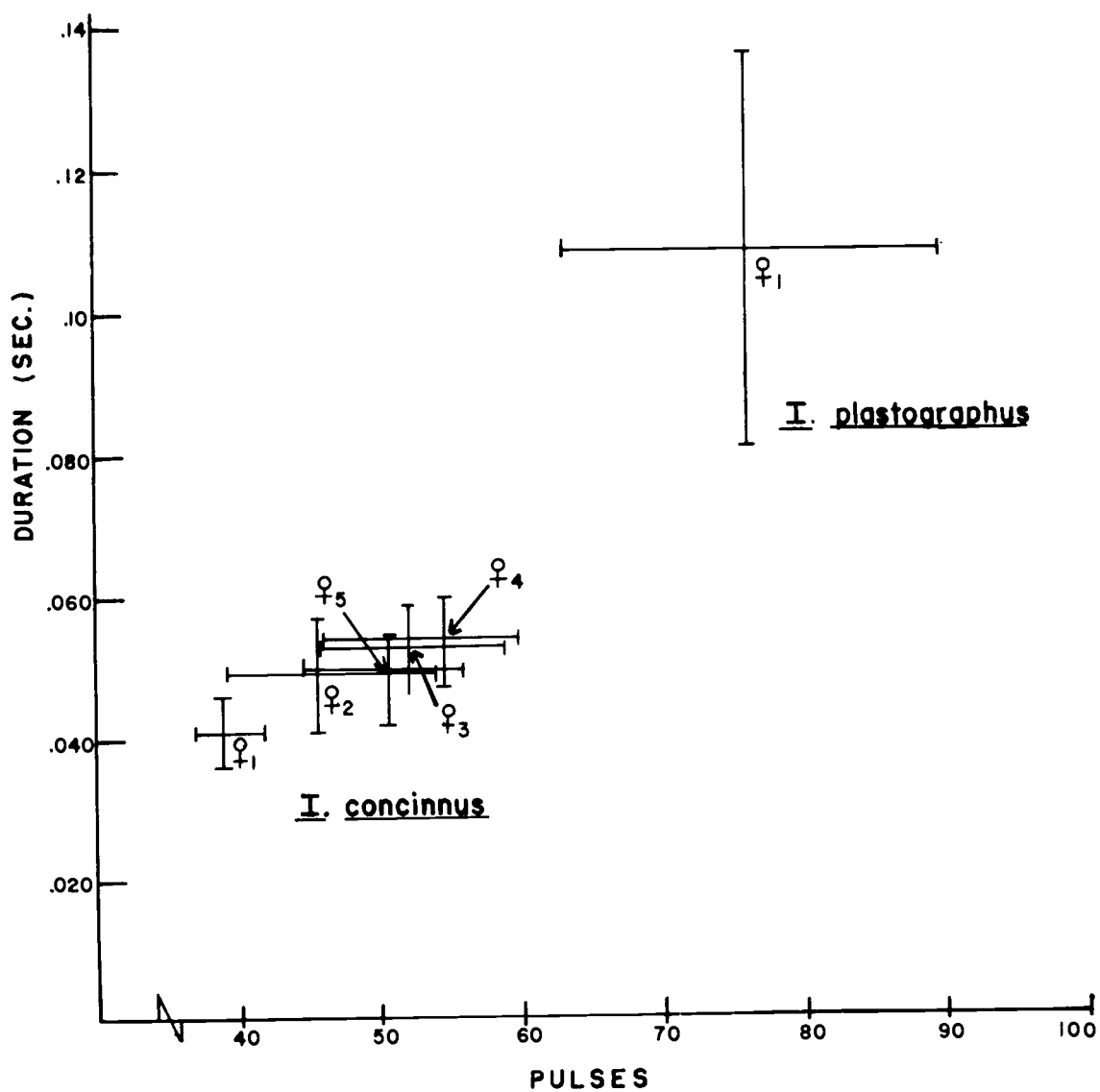


Fig. 11. Confidence intervals (95%) of chirp duration and number of pulses per chirp in the attraction context of Ips concinnus and Ips plastographus.

## IV. DISCUSSION

Ips t. tridens and I. concinnus inhabited the same micro-environment, colonized their host at the same time and were behaviorally similar during pair formation. These conditions are favorable for and could have contributed to the evolution of a species-specific chemical and/or acoustical communication system to maintain species isolation. Although biological field data were not attainable for I. plastographus, colonization time and niche habits probably overlapped with the two other species (Lanier, 1970). When overlap occurred, selection pressure on I. plastographus could have resulted in the development of similar mechanisms to prevent hybridization with I. concinnus or I. t. tridens.

Although the collections indicate that I. concinnus emerge slightly before I. t. tridens, under field conditions this difference may be moderated. The 1:0.97 (M:F) sex ratio for I. t. tridens supports unquantified statements that coastal populations of I. tridens in California are 1:1 (Bright and Stark, 1973). In both species male mortality during dispersal and host search could account for the discrepancy between emergence ratios and attack sex ratios. Interestingly, Cameron and Borden (1967) found that female Ips paraconfusus Lanier (= confusus LeC.) emerged in greater proportion at first, and males dominated later, which is opposite from the sex

ratio trend of I. t. tridens. The apparent lack of a sex ratio trend in I. concinnus may have been influenced by greenhouse conditions and/or the low number of beetles collected.

While the nature of these data is limited and log emergence does not reflect alternative overwintering sites, the mean sex ratio and dramatic sex ratio trend in I. t. tridens are probably real.

Although micro-anatomical measurements established statistical differences in several parameters between male and female I. concinnus, regression analysis related file length and number of ridges to beetle head size, and not sex. Male head width was significantly larger than female head width (Table 2), explaining, in part, the longer file length and greater number of ridges possessed by the male. This type of analysis may be relevant to measurement data comparing morphologically similar stridulatory organs in establishing a sexual, species or size related difference. Results here are reversed from that found in several Dendroctonus species where the pars stridens decreased in relative length as elytra size increased (Michael and Rudinsky, 1972). Because there was no correlation between the pars stridens ridge number and the stridulation pulse number among I. concinnus conspecifics, stridulatory organ measurement differences may be simply an expression of sexual dimorphism.

Comparisons of I. concinnus stridulation and stridulatory apparatus indicated that females can use their complete file to

produce chirps, but usually only  $1/4$  to  $1/2$  of the total file ridges are utilized. In contrast, males in the aggressive context never used more than  $1/4$  of their total ridges on the pars stridens. Thus, in this species, it seems appropriate to relate individual stridulation pulses to contact of the plectrum on separate ridges of the pars stridens.

The vertex-pronotum stridulatory organ of I. plastographus is a more complex structure than that found on I. concinnus and is more common in those Ips known to stridulate (Barr, 1969). Both parts of the stridulatory organ consisted of a series of ridges, preventing establishment of a causal relationship between single pulse production and pars stridens-plectrum contact. Except for a four fold distance increase between ridges on the pars stridens of I. plastographus, measured parameters of each stridulatory organ are similar to I. pini (Swaby and Rudinsky, 1976). This large difference is partially expressed in pulse rate, since the pulses in I. pini chirps can be produced at twice the rate of female I. plastographus chirps.

A distinct change in attraction<sup>2</sup> acoustic signals was not apparent as females of I. concinnus successively joined the male in

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<sup>2</sup>The attraction chirp was originally defined to denote stridulation evoked from Dendroctonus males stimulated by species specific attractants in female frass (Rudinsky and Michael, 1972). Recent preliminary data and observations indicate that females of this species may normally stridulate only when confronted with physical resistance when entering an attractive gallery; i.e. with the male removed stridulation generally does not occur (n=15). Attraction

the gallery. It should be noted, however, that the acoustic signals may be important indicators in explaining the mean attack sex ratio. With respect to this, three observations appear related: (1) the attraction chirp parameter values increase in a continuum through the male's acceptance of his fourth female (Fig. 6-8); (2) the chirps emitted when the first female joins the male have a statistically lower number of pulses per chirp than signals produced as later females enter (Fig 6); (3) the male displayed a substantially greater resistance to attracted females as he acquired additional family members. Conceivably, in times of rapid host colonization or high female populations, female gallery regulation could be a result of increasing male resistance. Energy expenditure necessary for the female to gain entrance under these conditions increases as family size increases and could partially or fully be responsible for the parameter trends of my acoustic results. Although this study does not conclusively explain the mechanisms involved in female regulation, it is interesting, and probably significant, that the mean field attack sex ratio (1:2.3 M:F) was correlated with the acoustic parameter trend. Male and female pheromone-acoustic interactions and their implications on pairing behavior or female gallery regulation remain to be established in this species, but may play an important role in host tree colonization.

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stridulation described here for Ips, upon reevaluation, may more appropriately be termed a pre-mating signal.

Similarities of chirp structure and sound parameters in the attraction behavioral context of I. concinnus indicate that sound production in this species is probably only of partial importance during pair formation, and is most likely combined with chemical, tactile and visual stimuli.

The fact that male acoustic response is quite distinct in length and pulse rate from attraction and stress sonic responses suggests that they may be functionally different.

The low sampling numbers for statistical analysis of I. plastrographus chirps may have influenced the intra-specific comparisons, and expanded analysis would be appropriate to fully clarify the results reported here. Interruption data, however, show rivalry chirps as structurally different, implying that the beetle may acoustically distinguish the rivalry category from attraction or stress.

The basic morphological differences in the stridulatory apparatus, when comparing the three species, presumably plays a significant role in acoustic response disparities. Stridulation pulse structure differences may be important in providing part of the communicative cues necessary to elicit a specific behavioral response in these beetles and may be explained by stridulatory organ morphology. Pulses within chirps produced by I. concinnus have a longer decay time when compared to female I. plastrographus, which may be due to the relatively dull plectrum rubbing against

broad ridges, whereas I. plastographus has a sound producing organ possessing relatively sharp ridges. However, resonating ability and rate of pulse production would also influence pulse structure.

Because a stridulatory organ was not found for I. t. tridens, pulse structure-stridulatory apparatus relationships cannot be considered.

I. pini stridulations were generally greater in all parameters measured, except duration and frequency, when compared to I. concinnus and I. plastographus (Swaby and Rudinsky, 1976). Distinct contrasts were not apparent in chirps produced by male D. pseudotsugae or D. ponderosae Hopk. (Michael and Rudinsky, 1972) when compared to I. concinnus, while male Dendroctonus valens LeConte produced acoustic signals substantially lower in number of pulses and pulse rate than female I. concinnus or I. plastographus, although comparable to male I. concinnus stridulations (Ryker and Rudinsky, 1976).

The statistical difference in duration and number of pulses, which appears to separate I. concinnus attraction chirps from I. plastographus, and the differences in the envelope and individual pulse structure found in I. t. tridens clicks are evidence that interspecific acoustic differences are present in the attraction context of these three sympatric species. It appears the three species could maintain their species integrity by means of acoustic signals, in probable combination with chemical and tactile stimuli. However,

this conclusion is based on the assumption that these species can perceive sonic signals and respond accordingly. Examination of inter- and intra-specific acoustic functions and chemical specificity would help to clarify this subject.

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