

AN ABSTRACT OF THE THESIS OF

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Title: Sound Production in *Leperisinus oregonus* Blackman and

L. californicus Swaine (Coleoptera: Scolytidae)

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Abstract approved:

Dr. Julius A. Rudinsky

Both *Leperisinus oregonus* and *L. californicus* are bark beetle species which emerge from *Fraxinus latifolia* brood logs as sexually immature adults and disperse to living ash. Occasional field observations suggest that, for overwintering and maturation feeding, *L. oregonus* enter trunks and branches, whereas *L. californicus* enter twig crotches, buds and even leaf axils. Reemerged beetles also make these short burrows. Not only *L. oregonus* but also *L. californicus* initiate egg galleries April through June, and *L. californicus* adults that overwinter as larvae infest ash in August. Sex ratios of both species at emergence and also when trapped in the field to cages containing naturally infested logs were usually 1:1. In Sept. 1975, *L. oregonus* emergence varied with maximum daily temperature. *L. californicus* produced F-1 and F-2 generations in the greenhouse when provided with cut twigs and logs. Excisions of field attacks confirm previous reports that both species are monogamous and that females initiate gallery construction.

The *pars stridens*, consisting of one file on the posterior medial undersurface of each elytron, showed bilateral, sex and species differences. The most notable were: left files shorter and wider than right files, females with fewer ridges than males, *L. californicus* with shorter files than *L. oregonus*. There was no species overlap in males'

left file ridge spacing, averaging $1.9\ \mu$ for L. californicus and $3.0\ \mu$ for L. oregonus. Three-variable discriminant functions could completely separate the four species-sex groups. First principal components accounted for 47 to 68 percent of variation within species-sex-side groups. Left and right file measurements were correlated within species-sex groups, but redundancy was only 33 to 59 percent. Number of ridges was correlated with file length, even after the effect of elytral length was removed, within species-sex-side groups. The plectrum, a pair of scrapers on the seventh tergite's posterior edge, is absent in females. The distance between scrapers was slightly but significantly greater in L. oregonus than in L. californicus.

In the laboratory, 25 of 50 L. californicus pairs mated while the male was on the bark surface at the female's gallery entrance, or partly inside the entrance. Based on 23 pairs, premating behavior averaged 16.4 min and copulation averaged 6.9 min. Most males of both species stridulated at conspecific female gallery entrances. In several instances, rival L. californicus males engaged in violent conflicts near attractive female galleries. In two cases, L. oregonus rivals gradually displaced resident males. Most male-male encounters were brief, and audiorecorded "rivalry" stridulation was similar to stress stridulation. Both were nearly continuous runs of short chirps. Premating and postmating stridulation consisted of intermittent series of longer chirps of alternating forms labelled "major" and "minor". Major chirps usually had similar numbers of toothstrikes but shorter durations and faster toothstrike rates than minor chirps. L. oregonus had faster series and premating chirp rates, shorter series durations, shorter minor chirp durations and fewer toothstrikes in both major and minor chirps than L. californicus. L. californicus had slightly but significantly faster chirp rates and shorter series durations after mating than before. Females were not heard to stridulate.

Sound Production in
Leperisinus oregonus Blackman
and L. californicus Swaine
(Coleoptera: Scolytidae)

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ERRATA

2nd pg. of abstract, line 23	labeled (not labelled)
2nd pg. of abstract, line 26	stress (not series)
pg. 3, line 17	which (not and)
pg. 3, line 20	1976b (not 1967b)
pg. 12, line 14	comma (,) after Bright
pg. 16, line 10	mesh (not meash)
pg. 19, line 7	brand (not branch)
pg. 19, line 13	cross out "for each species"
pg. 23, line 15	one (not two)
pg. 25, Table II, row 3	1:1.2 (not 1:1.5)
pg. 25, Table II, row 6	1:2.0 (not 1:2.0*)
pg. 36, line 25	period (.) after location
pg. 40, Plate I legend, line 9-10	right (not left)
pg. 44, line 9	hyphen (-) between species and sex
pg. 45, Table IV, row 7	522.2 (not 522.9)
pg. 60, line 25	or (not of)
pg. 69, line 5	comma (,) after in
pg. 77, Table XI, row 16	19.8 (not 25.8)
pg. 78, Table XIII, row 3	39.8 (not 29.8)
pg. 82, line 18	14...15...16 (not 13...14...15)
pg. 86, line 3	1976 than in 1975
	(not 1976 than in 1976)
pg. 86, line 11	refrigerator (not referigerator)
pg. 96, line 24	where it was (not were it was)
pg. 113, item 98	entomologische (not entromologische)
pg. 114, item 110	underline C.N.R.S.
pg. 115, items 127 and 128	umlaut over "o" in Schönherr
pg. 115, item 128	pheromone (not pheronome)
pg. 116, item 140	behaviour (not behavior)
	colonisation (not colonization)
pg. 117, item 157	98 (not 08)
throughout	$\mu = \mu m$, $F-1 = F_1$, $F-2 = F_2$

Corrections are submitted by Suellen Vernoff for insertion in the masters thesis: "Sound Production in *Leperisinus oregonus* Blackman and *L. californicus* Swaine (Coleoptera: Scolytidae)" commencement June 1979.

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SOUND PRODUCTION IN LEPERISINUS OREGONUS BLACKMAN
AND L. CALIFORNICUS SWAINE (COLEOPTERA: SCOLYTIDAE)

I. INTRODUCTION

Sound production in insects has been known, and its uses debated, for centuries (Haskell, 1961). An admittedly incomplete bibliography (Frings and Frings, 1960) contains 1752 references on insect sound production or reception, only three of which are on beetles of the family Scolytidae. Classical fields include morphology of acoustic and auditory organs, analysis of sounds, acoustic behavior, and hearing, whereas new areas of investigation include neural mechanisms and biophysics of sound production and reception (Michelsen and Nocke, 1974). The availability of new electronic recording and analyzing equipment following World War II has encouraged research and reviews on arthropod acoustics.

Communication, or "transfer of information from one organism to another," is demonstrated by an observable response in the receiving individual (Alexander, 1967). Chemical, visual, acoustic and tactile signals are prominent modes of communication, while factors such as temperature changes, substrate vibrations and microwave radiation may also play a role (ibid). In fact, electrical communication has just been reported in termites (Becker, 1977). In bark beetles of the family Scolytidae there are complex interactions of olfactory and auditory signals that influence behavior (reviewed by Rudinsky and Ryker, 1977).

Several reviews of current knowledge on insect sound communication have been made (Frings and Frings, 1958; Haskell, 1961; Busnel, 1963; Alexander, 1967; Michelsen and Nocke, 1974). Stridulation refers, in particular, to sound emission through "rubbing of two specialized surfaces against one another" (DuMortier, 1963a). It occurs in Orthoptera, Coleoptera, Heteroptera, Hymenoptera and less so in Lepidoptera, Diptera and other orders (ibid). Usually, the pars stridens (or "file") is the more complex structure where sound waves appear to originate due to mechanical excitation by the plectrum (or "scraper") (ibid). In most cases, friction itself does not produce

sound but is a mechanism of "frequency multiplication" involving vibration of the cuticle (Michelsen and Nocke, 1974). Structure and location of stridulatory organs follows superfamily divisions in Orthoptera, but the relationship is less clear cut in other orders (DuMortier, 1963a). In Coleoptera, different stridulatory mechanisms occur within a family, similar ones cut across family lines, but nearness or distance of genera within a family can sometimes be inferred from sound producing organs (Gahan, 1900). In Scolytidae, all species known to have an "elytra-abdominal tergites type" stridulatory apparatus in males belong to the subfamily Hylesininae, the "gula-prosternal type" is found in one or both sexes of Scolytus spp. (Scolytinae), and the "vertex-pronotal type" occurs in females of all but two of the Ips spp. (Ipsinae) known to possess stridulatory organs (Barr, 1969).

Calling songs of Orthoptera bring males and females together from a distance for pair formation. In Coleoptera, species-specific female calling chirps in two Tropisternus spp. (Hydrophilidae) cause locomotion and phonoresponse in conspecific males and are distinguished from other conspecific acoustic signals (Ryker, 1975). Possible calling signals have been reported in both sexes of several Tropisternus spp. (Ryker, 1972 and 1976). "Spontaneous" sounds of female Trox suberosus (Trogidae) may also serve this function (Alexander et al., 1963). Mampe and Neunzig (1966) demonstrated that male and female Conotrachelus nenuphar (Curculionidae) move to cages containing stridulating weevils of the opposite sex, but not to those containing the same sex or surgically silenced weevils. In Scolytidae, which produce only soft sounds, the calling function is taken by olfactory signals in the form of powerful aggregation pheromones produced by the gallery-initiating sex of many Dendroctonus and Ips spp. (Borden, 1974; Lanier and Burkholder, 1974) and Scolytus multistriatus (Peacock et al., 1971).

At close range, insect sexual behavior may be mediated by a variety of acoustic signals, both premating and postmating. Courtship signals occur after pair formation and culminate in copulation or insemination when the courted individual is sexually responsive (Alexander, 1967). In Coleoptera, Van Tassell (1965) found interspecific differences in premating tremulos of four Berosus spp. (Hydrophilidae) and suggested

that they play a role in courtship and species isolation. Ryker (1972 and 1976) reported a variety of male courtship signals in Tropisternus spp. and male signals during probing and copulation. Schuster and Schuster (1971) reported male and female courtship signals in some Passalidae. In Scolytidae, the gallery-joining sex (e.g. male Dendroctonus and female Ips) commonly stridulates while entering a breeding gallery initiated by the opposite sex. These signals have an "admittance function" in Ips calligraphus (Wilkinson et al., 1967) and I. confusus (Barr, 1969) and occur in the same situation in I. pini (Swaby and Rudinsky, 1976). Initial chirps produced at gallery entrances in six Dendroctonus spp. (Rudinsky and Michael, 1972; Michael and Rudinsky, 1972; Rudinsky, 1973; Rudinsky and Michael, 1974; Ryker and Rudinsky, 1976a, and others) are called "attractant" chirps, because they are elicited by attractive female frass and/or synthetic components of female attraction pheromones. In D. pseudotsugae, this signal is replaced after several minutes by one similar to the male rivalry chirp, and accompanies aggressive premating behavior in the gallery (Rudinsky and Ryker, 1976). Courtship chirps are produced just prior to mating by this species (ibid) and by D. ponderosae (Ryker and Rudinsky, 1967b). A female courtship signal occurs in Ips calligraphus (Wilkinson et al., 1967). Chirps of the gallery-initiating sex (Rudinsky and Michael, 1973; Oester and Rudinsky, 1975) are usually softer and smaller, but play a role in chemoacoustic interactions during premating (Rudinsky et al., 1976; Rudinsky and Ryker, 1977). Behavioral and field tests (Rudinsky, 1968 and 1969) and collections of chemicals emitted in response to stridulating beetles or electronic playbacks of tape-recorded chirps (Rudinsky et al., 1973, 1976 and 1977; Libbey et al., 1974) have demonstrated these interactions. Other work on pre-mating stridulation in scolytids has been done for three sympatric Ips spp. (Oester, 1977; Oester and Rudinsky, in press), Hylurgops rugipennis (Oester, Ryker and Rudinsky, in press), Polygraphus rufipennis (Rudinsky, Oester and Ryker, 1978) as well as Hylesinus oleiperda and Leperisinus fraxini (Rudinsky and Vallo, in press).

Acoustic signals are produced during aggressive interactions with conspecifics (DuMortier, 1963b), especially in elaborate male fighting

behavior of Gryllidae (Alexander, 1967). In Coleoptera, male fighting is accompanied by aggressive (Alexander et al., 1963; Schuster and Schuster, 1971) and defensive (Schuster and Schuster, 1971) stridulation in Passalidae. Stridulation accompanies female rejection of courting males in Tropisternus spp. (Ryker, 1972 and 1976). In Scolytidae, "rivalry" stridulation has been reported in female Ips spp. (Swaby and Rudinsky, 1976; Oester, 1977; Oester and Rudinsky, in press) and male Dendroctonus spp. (McGhehey, 1968; Rudinsky and Michael, 1974; Rudinsky and Ryker, 1976; Ryker and Rudinsky, 1976a and 1976b, and others). Rivalry chirps in Dendroctonus spp. can be elicited by mixtures of natural and synthetic components of pheromones released during male fighting (Rudinsky, 1973; Rudinsky and Michael, 1974; Rudinsky et al., 1974; Rudinsky and Ryker, 1976). Rivalry chirps are not distinct from chirps produced in attraction and stress (see below) contexts in Polygraphus rufipennis, one of the few polygamous members of subfamily Hylesininae (Rudinsky, Oester and Ryker, 1978) nor from stress chirps in male Leperisinus fraxini (Rudinsky and Vallo, in press).

Sounds emitted during handling by humans are known in almost every order of insects, but a function has not been demonstrated for them (Alexander, 1967). In Coleoptera, they have been reported from Hydrophilidae (Van Tassell, 1965; Ryker, 1972 and 1976), Curculionidae (Harman and Kranzler, 1969), Passalidae (Alexander et al., 1963; Schuster and Schuster, 1971), Cerambycidae (Alexander et al., 1963; Finn et al., 1972), Trogidae, Geotrupidae and Scarabaeidae (Alexander et al., 1963). In Scolytidae, they have been reported from Ips spp. (D. L. Wood, 1961; Wilkinson, 1962) and in addition to stridulation in other contexts from Dendroctonus, Ips, Hylurgops and Polygraphus spp., as already mentioned. In Leperisinus, these "stress" sounds have been reported from L. fraxini males (Knoche, 1904; Schönherr, 1970a; Rudinsky and Vallo, in press) and in unspecified contexts, probably stress, from L. fraxini (Wichmann, 1912; Marcu, 1931) and L. orni (Marcu, 1931).

The present study represents the first quantitative analysis of sound production in two North American Leperisinus spp. Four of its objectives were: (1) to confirm and supplement previously reported

biological information on L. oregonus Blackman and L. californicus Swaine; (2) to describe and compare the stridulatory apparatus of both species; (3) to describe behavior associated with stridulation during pairing and in other contexts; (4) to record, analyze and compare the acoustic signals of both species in stress, rivalry and premating situations. Since the work was descriptive rather than experimental, the communicative function of the described sounds was not demonstrated.

II. LITERATURE REVIEW ON LEPERISINUS REITTER

The genus Leperisinus was proposed by Reitter (1913) to include three European species of the genus Hylesinus Fabricius. L. fraxini is considered the type (Swaine, 1918). Currently, there are approximately 17 Leperisinus spp.: eight in North and Central America (confirmed by S. L. Wood, letter, Jan. 16, 1978), one each in Russia, India, Burma and New Guinea, and two in Australia (confirmed by Schedl, letter, Jan. 25, 1978). They are listed in the Appendix. Fossil evidence in North America consists of one Hylesinus extractus specimen from a Miocene Period formation in Colorado (Scudder, 1893) which is thought to represent an extinct or undiscovered genus closer to Polygraphus (Chamberlin, 1939 citing Hopkins). Much pre-1945 economic entomological literature discusses European Leperisinus spp. under Hylesinus, but North American authors have used the former name for over 60 years. The most common European species, L. fraxini, has been intercepted at least twice from packing crates entering Canadian ports (Munro, 1935; de Macedo, 1938).

Leperisinus spp. usually attack ash, including: F. latifolia (Chamberlin, 1958), F. pennsylvanica (Beal and Massey, 1945; McKnight and Aarhus, 1973), F. americana (Blackman, 1922; Doane, 1923) in North America; F. excelsior (Barbey, 1913 and many others) and F. ornus (Fuchs, 1906; Escherich, 1923 and others) in Europe; F. oxyphylla (Peyerimhoff, 1919) in North Africa; and F. excelsior hookeri and F. floribunda (Schedl, 1959) in India. Other hosts include Olea sp. (olive) in California (Essig, 1917) and Italy (Del Guercio, 1931; Russo, 1932); an unidentified desert shrub in Mexico (S. L. Wood, 1956); three very different hosts not resembling ash in Guatemala (S. L. Wood, 1967); and a variety of hardwoods in Europe. The latter include: Syringa vulgaris, Quercus pedunculata, Robinia pseudoacacia, Fagus sylvatica, Juglans nigra, Pirus malus, Ailanthus and Populus tremula (Reitter, 1913; Balachowsky, 1949; Karpinski and Strawinski, 1948 and others).

Biological information, other than geography and hosts, is absent except for L. fraxini and L. orni in Europe (including Russia), L. aculeatus and L. criddlei in eastern and midwestern United States and

Canada, and L. californicus and L. oregonus in western North America. The latter two will be discussed separately, at the end of this section.

Most authors state or imply that the genus is monogamous. Exceptions are Felt (1905) concerning L. aculeatus and Pfeffer (1955) concerning Hylesinus in general, who mention bigamy. Rudinsky and Vallo (in press) also observed two females present with one male. According to Chararas (1958), the L. fraxini female bores in first, is joined by the male, copulates in the entrance, and may mate more than once. Egg galleries are transverse biramous, with eggs laid singly in niches and larval mines emanating from them perpendicularly in L. fraxini (Escherich, 1923 and others), L. aculeatus (Beal and Massey, 1945 and others), and L. criddlei (McKnight and Aarhus, 1973). They are oblique, with densely packed larval mines, in L. orni (Fuchs, 1906; Simmel, 1924; Strand, 1963). Gallery systems score sapwood, often deeply (Swaine, 1918).

There are one to three generations per year, depending on locality, in L. fraxini (Balachowsky, 1949; Russo, 1932; Del Guercio, 1931) and L. aculeatus (Dodge, 1938; Blackman, 1922; Baker, 1972). Only one generation per year occurs where L. orni (Fuchs, 1906) and L. criddlei (McKnight and Aarhus, 1973) have been investigated. A sibling generation produced by reattack of reemerged parents should not be confused with a true second generation (Escherich, 1923). Young adults, at least of L. fraxini, emerge as sexually immature (Escherich, 1923; Chararas, 1956 illustration and 1958; Jamnicky, 1961 with illustration; Novak et al., 1974). In contrast, females have four to eight differentiated eggs per ovariole when starting breeding attacks (Jamnicky, 1961).

Adults hibernate in specially excavated bark burrows in living ash or olive trees. L. fraxini bores into boles and limbs individually, or a few together in tunnels branching from one entrance (Russo, 1932). This stimulates abnormal growth of callus tissue, which latter splits in all directions forming "ash roses" or "bark roses" (Barbey, 1913; Reitter, 1913 and many others). Reemerged females produce similar burrows for ovary regeneration (Escherich, 1923), and reemerged males

may enter and die in fresh branches or in old ash roses (Chararas, 1958). L. orni prefers thin twigs, especially at edges of buds (Fuchs, 1906). L. aculeatus sometimes enters at a mechanical injury (Knaus, 1886) but also uses uninjured healthy trees (Dodge, 1938). Its short tunnels result in irritation, causing an abnormal tissue condition (Blackman, 1922). L. criddlei enters outer bark around root collars of 4-6 inch DBH ash (McKnight and Aarhus, 1973). Larval overwintering was reported in L. fraxini (Simmel, 1924).

Varying statements have been made about host condition preference (for breeding attack) and importance of damage. L. fraxini was a pest in Ukrainian windbreaks (Schedl, 1943b) and killed young leaders in eastern European Fraxinus plantations (Novak et al., 1974). Escherich (1923) stated that they avoid fast growing young trees but attack older ones even if healthy. Hopf (1937, 1938) did studies on L. fraxini digestion and suggested that starch, contained in fresh ash but broken down in bark selected by the beetles for breeding, is less subject to breakdown by their enzymes than are some smaller compounds, but his work has not been repeated by others. Silvicultural control methods include debarking infested trees (Barbey, 1913), felling or girdling trap trees (Escherich, 1923), and destroying infested prunings in olive orchards (Del Guercio, 1931). In North America, L. aculeatus enters dying or felled ash (Sterrett, 1915) as well as injured trees, green bark logs or stumps (Blatchley and Leng, 1916 citing Hopkins) but is said to avoid healthy trees (Beal and Massey, 1945). In North Dakota, L. criddlei attacks felled or rodent-girdled trees, broken branches and portions of trees weakened by attacks of L. californicus (McKnight and Aarhus, 1973). Unlike the latter species (in that area), its galleries are never blue-stained, "presumably because of the drier tissue," and lack ventilation holes, and larval mining is symmetrical above and below the egg gallery (ibid).

The only other recent research articles have been on L. fraxini. Digestive systems and male and female reproductive systems were described and illustrated (Chararas, 1956). A fungal disease was discovered and confirmed (Chararas, 1957). Temperature tolerance was determined as optimum at 17-30°C, torpor under 5°C and over 40°C, and

lethal under -20°C and over 53°C (Chararas, 1958). Three to four spring flight waves were monitored during 41-52 days, and female ovary development was followed during maturation (Jamnický, 1961). Attack density affected larval mortality and helped regulate the population (Jamnický, 1962). Life cycle research has been done on parasitic mites (Kielczewski and Seniczak, 1972 - on L. orni also) and parasitic Trichogramma chalcids (Michalski and Seniczak, 1974). Schönherr (1970b) reported field evidence that males produce an aggregation pheromone, but Rudinsky and Vallo (in press) have field evidence that it is produced by females. Acoustic signals of L. fraxini have already been mentioned. Rudinsky and Vallo (in press) photographed the male plectrum and pars stridens and measured the latter. English summaries of literature in the Review of Applied Entomology (1913-1977) indicate extensive but not intensive work on European Leperisinus, which will not be reviewed here.

L. oregonus Blackman (1943) was described from northwest Oregon on Fraxinus oregonus Nuttall. (now F. latifolia Benth. - Chamberlin, 1958). The only biological study was done by Underhill (1951) in northwest Oregon, especially around Corvallis. The species is monogamous. The female initiates a breeding gallery in felled trees in mid to late May and is joined by the male. Together, they excavate a biramous transverse gallery which is kept clear of frass. Eggs are laid singly in small niches on both sides of each fork, from which larvae bore perpendicularly, gradually widening their mines until pupation. Young adults emerge between mid Aug. and mid Oct. and on warm days in winter. They construct irregularly shaped, 7-13 mm long overwintering burrows in the bark of 5-7.5 cm diameter, lichen-covered limbs of healthy ash trees. Chamberlin (1958) included Washington in this species' geographical range.

L. californicus Swaine (1916) was described from California on olive and on brush in the chaparral belt. This species "has never been abundant enough to be considered a pest" (Bright and Stark, 1973) but has caused local problems. In California olive orchards, it injured and sometimes girdled trees, preferring sickly or dying trees or dead prunings but also entering vigorous trees through sunburned

or wounded spots (Essig, 1917). On the Stanford University campus in California, it attacked Fraxinus americana shade trees, beginning in smaller branches but progressing to the trunk, deforming older trees and killing young ones (Doane, 1923). In North Dakota, it attacked F. pennsylvanica used for shade, wildlife habitat, and protection against wind, snow and noise (McKnight and Aarhus, 1973). It killed branches, tops and even whole trees. Its hibernation chambers were in the outer bark of boles and contained one or more beetles. Adults attacked in late May to early June and made ventilation holes above their egg galleries, which were darkly stained with Ceratocystis fungus. Brood development caused sunken, discolored bark. Emergence was in Aug. (ibid)

Although F. pennsylvanica and F. latifolia are both in the "green ash group" (Sterrett, 1915), the life cycle described by Underhill (1951) for L. californicus infesting felled Fraxinus (latifolia?) in northwestern Oregon is quite different. Most overwintered as larvae. Emerged adults "wandered over the bark for several days before starting new galleries" in July through Sept. Attack by mid June was exceptional. Underhill observed no large migration of L. californicus, whose gallery systems were indistinguishable from those of L. oregonus. L. californicus males deserted the galleries shortly after copulation, which was not actually observed. In the laboratory, adults of this species emerged from brood logs, were provided with host material in metal boxes with light jars, destroyed irregular areas of bark and cambium while feeding, but did not reproduce. Essig (1958) names Oregon ash as the host in New Mexico, California and Oregon. Chamberlin (1958) includes Washington in the geographical range of L. californicus. Bright (1976) states that it occurs in western United States east to Texas and North Dakota and in the southern parts of Manitoba and Saskatchewan in Canada. Nematode parasites or associates of this species are discussed by Massey (1971 and 1974). A hymenopterous parasite was found by Essig (1917). Nematodes, hymenopterous parasites and two mite species, one predatory and one eating fungus growing in borings of larval mines, are associated with either L. californicus or L. oregonus in Oregon (Underhill, 1951).

Barr (1969) included L. californicus males among scolytids with an "elytra-abdominal tergites type" stridulatory apparatus. The pars stridens, or files of parallel transverse ridges near the apices and sutural margins of both elytra, had been partially described for L. fraxini (Wichmann, 1912; Kleine, 1921; Marcu, 1931) and L. orni (Marcu, 1931), but these authors had incorrectly considered setose areas on the seventh tergite to be the plectrum (Barr, 1969). Experimental evidence proved these areas to be nonfunctional in stridulation of other Hylesininae (Barr, 1969). Two tergal processes, each with a stout seta, on the posterior margin of the seventh tergite function as a plectrum, and Barr found them to be further apart in L. californicus than in two Dendroctonus spp. which she examined.

III. METHODS

Species and sex discrimination

The two Leperisinus spp. can be reliably distinguished by pleural setae on the prothorax, which are "elongate and simple" in L. oregonus but "somewhat scalelike and palmately divided into from three to seven elements" in L. californicus (S. L. Wood, letter, March 28, 1975). Antennal clubs are elongate and conical with three distinct sutures in L. oregonus but oval and compressed with two distinct sutures in L. californicus (Chamberlin, 1958). After some experience, color pattern differences were obvious, except in old beetles with scales rubbed off, but decisions made on this basis were confirmed by checking the prothorax.

L. californicus was sexed by frons topography and by scales on the elytral declivity (Underhill, 1951; Bright 1976). Males have a concave frons. Females have a flat or convex frons with a small but definite median carina. Males have "larger and more spatulate" (Underhill, 1951) scales on the medial interspace of the posterior third of each elytron. In females, these scales are only slightly longer than more lateral ones and do not project much above them.

L. oregonus was sexed by color pattern on the elytral declivity. Blackman (1943) mentioned that males have "yellow scales more numerous" and "elytral interspaces with larger asperities" than females. I did not notice the latter character but found color pattern to be 99 percent effective, except in old beetles with scales rubbed off. The female elytral declivity appears dark brown to black with two white or tan "eye-spots" where the fourth, fifth and sixth interspaces meet and end. A light line posterolateral to the eyespot occurs on the ninth interspace on each side. Often, a patch of reddish and/or lightly colored scales is on the medial interspaces between the eyespots. Rarely, females have additional light scales. Frass or waxy material should not be mistaken for light scales. Males have lightly colored but mottled declivities. Dark markings occur on the medial interspace slightly anterior to the ends of interspaces four through six, and on

the medial interspace from shortly behind the first marking to the elytral tip. Other small patches of dark scales vary in size and location among individual males. Difficult specimens can be checked by forcing the beetle's abdomen out from under the elytra, revealing the arrangement of posterior abdominal tergites typical of subfamily Hylesininae (Plate III, A for males, F for females).

Biological observations and collection of beetles

Field work was done within ten miles of Corvallis, Oregon at:

Oak Creek	T11S R5W Section 18 SE quadrant
Jackson Place	T11S R5W Section 15 NW quadrant
Soap Creek	T10S R5W Section 24 center
Berry Creek	T10S R5W Section 9 SE quadrant
Turkey Farm	(NW Harrison Blvd. between 36th and 53rd St.)

All but Oak Creek and Berry Creek were relatively pure ash stands. Only Soap Creek had more than a narrow windbreak of ash.

Three Fraxinus latifolia Benth. (the largest 24 cm DBH) were felled on April 22, 1975 at Soap Creek for observation of spring breeding attack. Leperisinus were collected during colonization by gently knocking them, using soft forceps, into individual gelatin capsules. The capsules were placed in tins in an ice chest. The disadvantage of picking Leperisinus off logs is that many (most?) escape notice. In 1975, an unusually high sex ratio (4.4 males to one female) was obtained for L. oregonus collected this way. This may have been due to the lighter, possibly more conspicuous coloration of males, to females going directly to the underside of the felled tree rather than wandering, or it may have reflected the actual sex ratio near the end of this species' flight period. Beetles collected from these ash in late May and early June, 1975 were used for behavioral observations and audiorecordings. When not in use, live beetles were stored in metal tins with crumpled pieces of moist paper toweling in a refrigerator at about 4°C.

Another method of obtaining attacking Leperisinus was to place infested ash logs in a cage on a plywood platform in an ash stand and collect beetles which flew to the cage. Cages were 56 x 61 x 86 cm (sometimes larger) wooden frames covered by fine wire (sometimes

plastic) mesh. Logs used on Aug. 4, 1975 were from a small ash felled July 30 and infested through Aug. 3. On Aug. 9, 1975, another cage was filled with infested branches of a tree felled July 14. Collections were made from both cages on Aug. 9-12 and 14. On April 23, 1975 an ash (28 cm DBH) was felled for infestation. Two basal logs from this tree were placed in a cage with five (winter cut) logs which were heavily chopped with a chisel to expose possible host odors on May 9, 1976 for collection of beetles that day. After infestation was well under way, on May 26, 1976, 13 other logs from this tree were placed in four cages, and the tops removed from the site, for collection that day. On Feb. 27, 1978, two ash (21 cm and 27 cm DBH) were felled for infestation. Five small infested logs and many branches were caged on May 7, 1978 for collection of beetles on May 7-8. Most work was done at Soap Creek. Only the winter cut logs used on May 9, 1976 and logs used in 1978 were from Turkey Farm, and collections on those dates were on that site. The L. californicus males and all but one female used in 1976 audiorecordings came from the May 26 Soap Creek collection. Some L. californicus used in 1976 behavioral observations, without audiorecording, came from additional collecting (May 26) at Turkey Farm from caged infested logs, infested branches covered with black plastic, and (very few) from cages with uninfested logs or logs into which L. californicus had been artificially introduced. Beetles were collected individually in gelatin capsules in 1975 and 1976. The reason for collecting Leperisinus during attack, rather than simply placing brood logs in the greenhouse and collecting the emerging new generation, is that young adults of these two species are sexually immature. They disperse to undergo maturation feeding in living ash before aggregating to establish breeding galleries. Stridulation and associated behavior of immature adults may occur but was beyond the scope of this study.

For observation of emergence, the largest of the three Soap Creek ash felled April 22, 1975 was bucked into 36 sections, each 34-37 cm long, on Aug. 11, 1975. On that day they were numbered consecutively with respect to their distance from the basal cut, transferred to the Forest Insect Lab Nursery, and placed in order (one to four per box) in

38 cm³ galvanized metal emergence boxes. Each box had a light jar made of a one-quart canning jar whose bottom was removed and replaced with fine (12 holes per cm) plastic mesh, for aeration. The boxes were shaded by the north wall of the greenhouse. Collections of emerging Leperisinus were made between Aug. 14 and Oct. 19, 1975. They were made daily between Aug. 31 and Oct. 1, 1975. Emerging Hymenoptera were collected during this period and in June, 1976, but not regularly. Other logs with particularly heavy infestations of L. oregonus were found at Soap Creek and used to supplement emergence. On Sept. 9-11, 1975, hourly collections were made from selected high-yielding emergence boxes and hourly shade temperature recorded. Daily temperature data were provided by the OSU Dept. of Atmospheric Sciences. In Sept., 1976, the length, basal DIB and apical DIB of each log from the main tree was measured before they were debarked and the number of galleries counted. Galleries were not measured, since the tree contained a mixture of two Leperisinus species. Some emerging beetles were killed in hot water (near boiling) and preserved in 70 percent ethanol for morphological studies.

To simulate natural overwintering conditions and to obtain sexually mature L. oregonus, several hundred were placed outdoors in "sleeve" cages constructed around 7-13 cm diameter boles of living ash saplings at Jackson Place. The sleeves were about 60 cm long, one or two per tree, and less than two meters above the ground. Plastic mesh sleeves did not hold together, because plastic tape did not stick to this material. Cotton sleeves were durable, but had to be provided with an air space to prevent molding after rain. This was done by building up 2.5 cm rings (of carpet scraps and tape) around the upper and lower ends of each bole section. The cloth was fastened to these rings instead of directly to the bole. L. oregonus adults (emerged Sept. 19-22, 1975 from Soap Creek logs) were confined, sexes separately, 30-40 per sleeve (on Sept. 26 and Oct. 5, 1975). At this time, a mixture of yellow and brown with green leaflets indicated that the saplings were partly dormant. The beetles bored into the bark, and were excised and dissected in spring, 1976. The last group to be excised was used for 1976 behavioral observation and audiorecording.

Early in the study, efforts were made to enable Leperisinus to undergo maturation feeding in the greenhouse. Infested ash logs from a tree felled in spring, 1974 at Oak Creek were stored in the walk-in cooler at 4°C from early Sept., 1975 until Jan. 27-28, 1975, when they were placed in the greenhouse. On Feb. 1, 1975, 19 ash sprouts were placed in jars of water on a greenhouse table, so that emerging beetles, mainly L. californicus, could feed. They soon bored in, but galleries were not examined until after three weeks. In the other greenhouse, a coarse wire mesh cage 183 x 99 cm² x 183 cm high was lined with white drapery cloth in lieu of fine mesh. On Jan. 29, 1975 and in early Feb., the following items were placed inside: five large Oak Creek brood logs, described above; four uninfested 5-14 cm diameter thin-barked logs, whose ends were dipped in paraffin, from an ash which was felled in fall, 1974 and bucked into 75 cm long sections and brought to the laboratory on Jan. 24, 1975; three bunches of ash sprouts in crocks of water; and six shallow boxes with ash litter (two), soil from beneath ash litter (two) and Douglas fir litter (two). The Oak Creek brood logs were removed on March 27, 1975 and L. californicus (280) collected over the next two weeks (March 28-April 9) for preliminary behavioral observations and for two audiorecordings. The litter was removed on April 6, 1975 and processed through Berlese funnels. The number of feeding scars on the sprouts was counted when the cage was emptied. Emergence and subsequent manipulations of an F-1 generation produced in the thin-barked logs are covered in the RESULTS section. Greenhouse temperature varied from 12°-28°C in late March. It was lower in fall, 1975, while the F-2 was developing and the heat had been shut off.

Morphological studies

Specimens preserved in 70 percent ethanol were prepared for scanning electron microscopy using Genesolv-D standard grade trichlorotrifluoroethane as an intermediate fluid, Freon-13 as a transition fluid in a Bomar SPC-900 critical point dryer, and a Varian model VE-10 vacuum evaporator to coat them with a 60:40 gold-palladium alloy. Scanning

electron micrographs were taken on an ISI mini-SEM model MSM-2 using Polaroid black and white land pack film type 55 P/N.

For light microscopy, 26 specimens were taken from each of four "species-sex" groups: L. oregonus males, L. oregonus females, L. californicus males and L. californicus females. Seventh tergites were dissected from males and their central areas mounted in Hoyer's solution on glass slides. Distance between scrapers was measured from the base of the seta on each of the two processes using a 10X American Optical filar micrometer eyepiece on a Bausch and Lomb compound microscope (430X). Elytra of both sexes were removed, and their lengths were measured using the same filar micrometer on a Spencer dissecting microscope (10X). "Inside length" (muscle attachment to tip) was measured for comparison with published dimensions of Dendroctonus spp. (Michael and Rudinsky, 1972). "Outside length" (crenulations to tip) was also measured, because it seemed less ambiguous on Leperisinus specimens. Elytra were then bleached and softened in 25-35 percent aqueous Chlorox[®] and their tips cut off and mounted, undersurface up, in Hoyer's solution on glass slides. Care was taken to avoid overbleaching. Each slide had both left and right elytral tips of one beetle. Number of file ridges, file length, file width and distance across 30 central ridges (perpendicular to the ridges) were measured on an American Optical compound microscope (450X) with the filar micrometer. Since ridges on the right file slanted, two width measurements (perpendicular to the median axis and parallel to the ridges) were taken on this side. "Ridge spacing" was calculated as 1/30 of the distance across 30 central ridges. "Ridge density" was calculated as a ratio of the number of file ridges over file length in mm.

Behavioral observations and audiorecording

Females were introduced into ash logs from trees which were felled and allowed to transpire for several days. The log surface was shaved slightly to level it. Three methods of confining females individually were used: a hole drilled in the bark over which a piece of wire mesh was fastened (Swaby and Rudinsky, 1976); a mini-cage made of plastic

tubing 2.5 cm diameter and 2.5 cm long, closed with wire mesh at one end and fastened to the log with putty or modeling clay (similar to Goeden and Norris, 1964); a gelatin capsule half fastened to the log with a pin (Barr, 1969) and/or modeling clay. Sometimes a hole was drilled into the bark before the female was placed under the mini-cage or gelatin capsule half. Some females escaped and reintroduced themselves into another location (always a bark crevice) or were reintroduced into a razor cut in the bark under wire mesh. A fourth method of introduction was to release females in a large cage containing an uninfested ash log. Females usually were in the log two to six days (18 hours to 18 days or less) when males were presented to them. Beetles usually were 2.5 to 14 days old since collection (up to 42 days). In general, beetles were held for fewer days in 1976 than in 1975. See the Appendix (Tables XXVI and XXVII) for individual method listings.

The easiest way to present males to females in galleries was to take a male directly from a tin on an ice pack and place him near a female's gallery entrance under a gelatin capsule half. After wandering for about a minute, the male seemed to "calm down," located the entrance and kept his head at or inside of it. At that point, he was not disturbed either by removal of the capsule and positioning of the microphone or by proximity of a hand lens. Walkways (Jantz and Rudinsky, 1965) were tried, but the small Leperisinus males often climbed the glass slides forming the walkway sides or the pins holding them up, or crawled underneath the slides if the bark was not quite level. A "tactile" walkway, made by cutting an artificial crevice leading to the gallery entrance, sometimes worked.

For stress recordings, males were hand held or, in one instance, pinched between the log and the microphone. Four of six L. californicus and one of five L. oregonus had previously been observed at female galleries but left, either on their own or after a (human) disturbance, and were recaptured and hand held. "Rivalry" recordings were made with two conspecific males either at a female gallery entrance, one behind the other in a drilled hole in the bark, or face to face in an artificially enlarged bark crevice (see the Appendix (Table XXVIII) for individual method listings). Many pairs of males in these situations produced few

or no chirps, while others produced chirps more like premating stridulation in situations explained in the RESULTS section.

Males were recorded using a Hewlett-Packard model 15119A condenser microphone, a PAR model 113 low noise preamplifier with a bandwidth set at .3-100 kHz and 5K amplification, a Nagra 4.2L recorder which exhibits an essentially flat measured frequency response from .22-22 kHz at a tape speed of 38 cm per sec, and Scotch[®] branch low noise 1.5 mil magnetic tape.

Major frequency bandwidths were estimated from audiospectrographs made with a Kay Electric Company 6061A Sona-Graph which is sensitive to .085-8 kHz, or .34-32 kHz when tape is input at quarter speed. Only one audiospectrograph was made from each of four recordings, one of male stress stridulation and one for each species of male stridulation at a female gallery entrance for each species. Since frequency spectra were wide and no differences between species or situations were apparent, the matter was not pursued.

Extensive analysis of amplitude modulation patterns was done using a Tektronix model 5103 N storage oscilloscope. For illustration only, oscillograms were made with a Tektronix C-5 polaroid oscilloscope camera using Polaroid black and white land pack film type 107. Measurements were made while the sound was "stored" on the oscilloscope screen. A random number table was used to choose chirps in every recording, series of alternating major and minor chirps in premating and postmating recordings (see RESULTS section for definitions), and starting chirps of two-second intervals in stress and "rivalry" recordings. Postmating stridulation was sampled separately from premating stridulation. Major and minor chirps of the same male were numbered separately and chosen independently of each other and of the series. In general, sample sizes were: 15 chirps per male for each chirp type and/or behavioral context, 10 series per male (20 if he made both premating and postmating chirps), and 10 two-second intervals per male. See Tables XI-XIII for numbers of chirps and males sampled in main categories and the Appendix (Tables XXIX-XXXVIII) for details. For each chirp, toothstrike number was counted, duration measured, and toothstrike rate calculated as a ratio of number of toothstrikes per chirp over chirp duration in sec.

For each series, chirp number was counted, duration measured, and chirp rate calculated as a ratio of number of chirps per series over series duration in sec. For each two-second interval (in a continuous run of chirps), number of chirps was counted and then halved to obtain chirp rate.

In some series, "hesitations" of .125-.375 sec occurred, and adjustments were made to compensate for them. The 33 series involved were in six L. californicus samples, four premating and two postmating. There were one to five hesitations per series ($\bar{x}=1.8$). A gap smaller than .125 sec was ignored and a gap larger than .375 (preferably over .5) sec was considered to be between two series. The usual gap between chirps (estimated for each male) was subtracted from each of his "hesitations," after which the total duration of "hesitations" within a series was subtracted from the series duration. Adjusted values were used for statistical analyses and included in species-situation group means.

Adjustments were also made to compensate for "skipped" minor chirps in one L. californicus premating sample. Only two series were involved, with two and three "skipped" chirps added per series.

One L. oregonus consistently "skipped" minor chirps and was neither used for statistical analyses nor included in premating group means.

Atypical chirps which occurred in reasonable numbers were sampled separately from typical chirps. However, they were still counted in the number of chirps per series if they occurred in these groupings.

Statistical analyses

The following analyses were run on morphological data: one-way and two-way ANOVAs, Scheffé multiple comparison tests, paired and unpaired t-tests, one-way and two-way MANOVAs and plots of discriminant functions, tests for additional information using results of MANOVAs on reduced models, paired and unpaired Hotelling T^2 tests, principal component analyses, multiple partial correlation and canonical correlation. Preliminary tests included Kolmogorov-Smirnov tests for

goodness of fit to the normal distribution, which did not show significant departure from normality within any species-sex group for any variable, as well as Bartlett's and F-max tests for homogeneity of variances, which showed significant but not marked heteroscedasticity in ca. half the variables.

Simple analyses run on emergence, trapping and some behavioral data included simple linear regressions, chi-square tests and paired t-tests.

The following analyses were run on acoustic data: simple linear regressions, two-way and nested ANOVAs (with corrections, where necessary, for unequal sample sizes), Mann-Whitney U-tests, a stepwise test procedure based on U (Sokal and Rohlf, 1969, pp 395-397), and Student-Newman-Keuls procedure for multiple comparison tests involving unequal sample sizes (using mean square for males rather than mean square for error). Preliminary F-max tests indicated marked heteroscedasticity among males. Consequently, ANOVAs were run on both untransformed data and their rank transforms (Iman, 1974; Conover and Iman, 1976). Since results were similar, even when heteroscedasticity was reduced, outcomes of analyses on untransformed data are presented in the thesis.

IV. RESULTS

Biological observations

Introduction

L. oregonus and L. californicus excavated breeding galleries on the underside of ash logs along the full length of felled, prostrate trees. They attacked all sides of the moss-covered basal section of a felled tree, of hung-up material in shady areas, and of logs in loosely stacked firewood piles. In a dense stand, old Leperisinus gallery systems were found on standing dead trees. L. californicus breeding galleries even occurred in branchlets and twigs of slash piles. The main criterion seemed to be that the bark be succulent, although not too sappy, and therefore still whitish. The beetles avoided bark that had become dry, hard and reddish due to exposure to direct sunlight. Co-inhabitation of the host by L. oregonus and L. californicus occurred in May and early June, but almost all those attacking from July through Sept. were L. californicus. Their attack, emergence, maturation feeding habits and hymenopterous parasites or associates are discussed below.

Attack

L. oregonus had a large flight in late May and early June, 1975. During this period, especially on May 28, hundreds of L. oregonus landed on ash trees felled April 22. L. oregonus attacks were found as early as May 16 in 1975, May 3 in 1976 and April 9 in 1978. An exceptionally late pair was found with brood on Sept. 2 in an ash felled July 14, 1975.

L. californicus attacks were found as early as May 16 in 1975 and May 3 in 1976. In 1978, one was caught on a log pile on April 10 and an attack which was well under way was found on April 27. The May attack on trees felled April 22, 1975 was smaller than that of L. oregonus. However, most galleries in trees felled between May 29 and July 30, 1975

were found to be occupied by L. californicus. An L. californicus pair just starting its attack was found on Sept. 2, 1975.

Underhill (1951) considered the L. californicus spring flight to be small in the vicinity of Corvallis, Oregon. However, in 1976 this species' May flight was sizeable. L. californicus predominated over L. oregonus in the irregular (23-38 cm long, 28 cm diameter) thick-barked butt section of a tree felled April 23, 1976 which was examined on May 10 (Table I). These galleries were in early stages of excavation. The 13 L. californicus galleries with eggs had one to six eggs each, and the L. oregonus gallery with eggs had five. A large spring flight of L. californicus was also observed on May 18-20, 1978.

Table II shows the numbers of L. californicus which landed on cages containing ash logs and branches infested mainly with breeding pairs of this species. Sex ratios differed only slightly from 1:1 ($.025 < P < .05$) on two of the eight days. Fig. 1 shows the temporal distribution of L. californicus caught on some of those days. There was always a drop in numbers towards sunset. Peak collections were in mid to late afternoon, except at Turkey Farm on May 9, 1976, where a strong wind began by 4:40 P.M. In general, the beetles flew on hot days (over 23°C). Few L. oregonus were trapped to cages containing infested ash logs. Probably, they were infesting other material in the ash stands during May, 1976 -material which was not located before the trapping experiments and therefore not utilized for these tests.

TABLE I. PROGRESS OF GALLERIES EXCISED FROM BUTT OF ASH ON MAY 10, 1976

Extent of gallery construction	Empty, or beetle lost	<u>L. californicus</u>			<u>L. oregonus</u>			Total
		Male alone	Female alone	Pair	Male alone	Female alone	Pair	
Wholly in bark	9	0	14	3	0	4	1	31
Scores sapwood but does not bend	6	1	4	27	1	1	6	46
Scores sapwood and bends and/or has eggs or egg niches	2	3	3	44	0	0	5	57
Total	17	4	21	74	1	5	12*	134

*Extent of the gallery of a 13th L. oregonus pair was not noted.

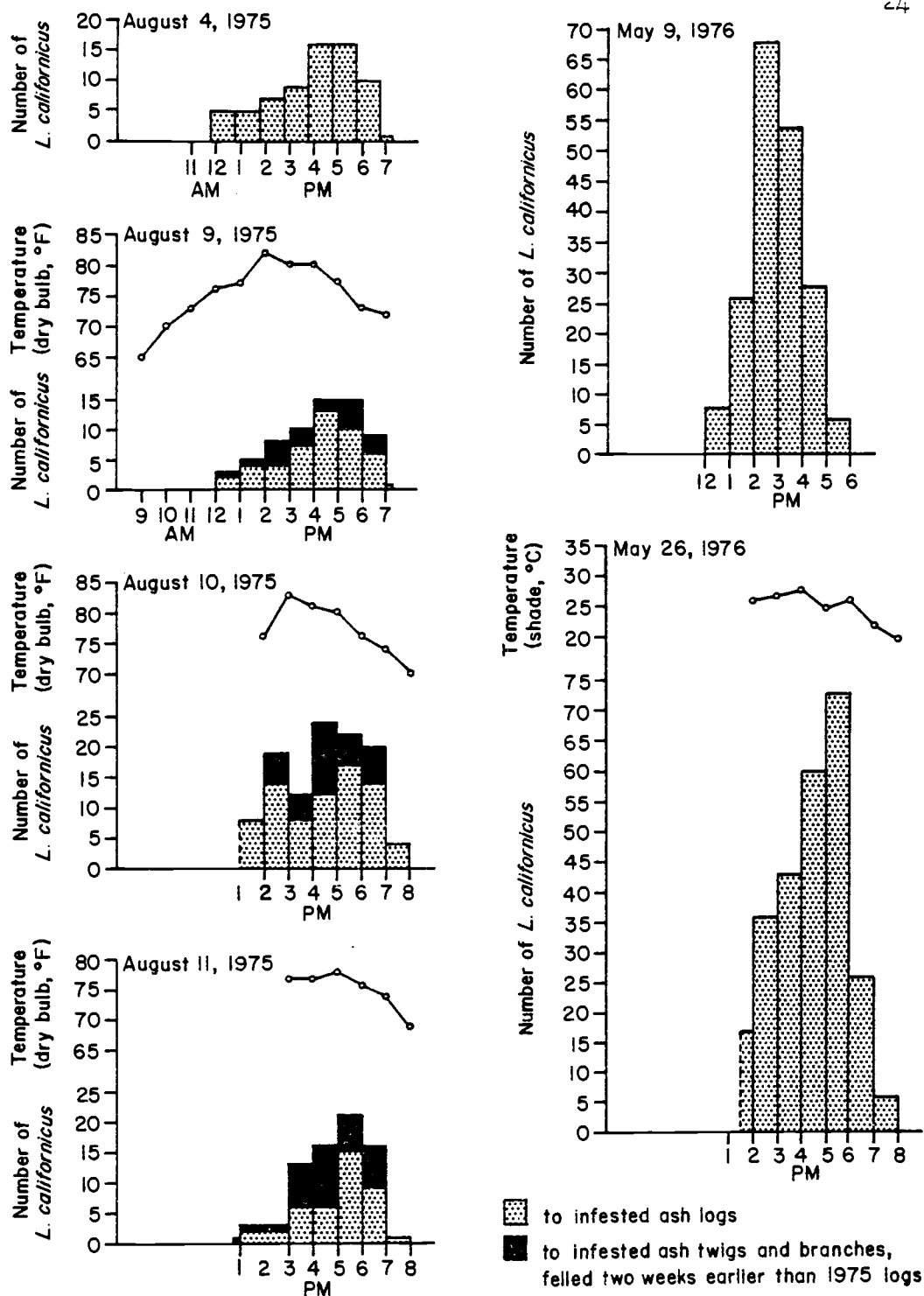


Fig. 1. Temporal distributions of *L. californicus* attracted to cages containing ash naturally infested with mainly this species. (Daylight savings time)

TABLE II. SEX RATIOS IN L. CALIFORNICUS TRAPPED IN ASH STANDS

Date	Site	Number of males	Number of females	Total	Ratio of males to females
Aug. 4, 1975	Soap Creek	36	33	69	1:0.9
Aug. 9, 1975	Soap Creek	26	40	66	1:1.5
Aug. 10, 1975	Soap Creek	50	59	109	1:1.5
Aug. 11, 1975	Soap Creek	27	44	71	1:1.6*
Aug. 12, 1975	Soap Creek	12	18	30	1:1.5
Aug. 14, 1975	Soap Creek	7	14	21	1:2.0*
May 9, 1976	Turkey Farm	88	103	191	1:1.2
May 26, 1976	Soap Creek	117	144	261	1:1.2

*Significantly different from 1:1 using Chi-square test ($P=0.05$)

L. oregonus were trapped to a cage containing infested ash on May 7 (37 males, 31 females, sex ratio 1:0.8) and May 8 (10 males, 18 females, sex ratio 1:1.8) in 1978 at Turkey Farm. Neither sex ratio was significantly different from 1:1. Fig. 2 shows the temporal distribution of L. oregonus trapped on May 7 and May 8, 1978. Few L. californicus came to the cage on those days. One log from the cage was examined (May 17) and found to contain mostly L. oregonus (32 pairs, 13 females alone in short galleries, 4 females alone in longer galleries with eggs) and only a few L. californicus (2 females in galleries with eggs, 1 male alone). The above mentioned log and the small branches were removed but the other logs left in, after which some L. californicus and few L. oregonus landed on the cage (May 18 and May 19, 1978).

These data support Underhill's (1951) observation that both L. californicus and L. oregonus are monogamous in this area. Additional field observations showed that some males were still present with the female when larvae, pupae and parasite immatures had developed in their gallery systems. Other males abandoned galleries early, or possibly never entered. Single beetles were most frequently female; less than one in five was male. After a pair was formed and the attack had progressed, a reddish ring of frass mixed with sap usually accumulated around the entrance and narrowed it. In any excised pair in which the two members' positions were noted, the male was nearer to the entrance. Underhill (1951) was probably correct in stating that in our Leperisinus spp., females initiate the galleries and are joined by males, and that

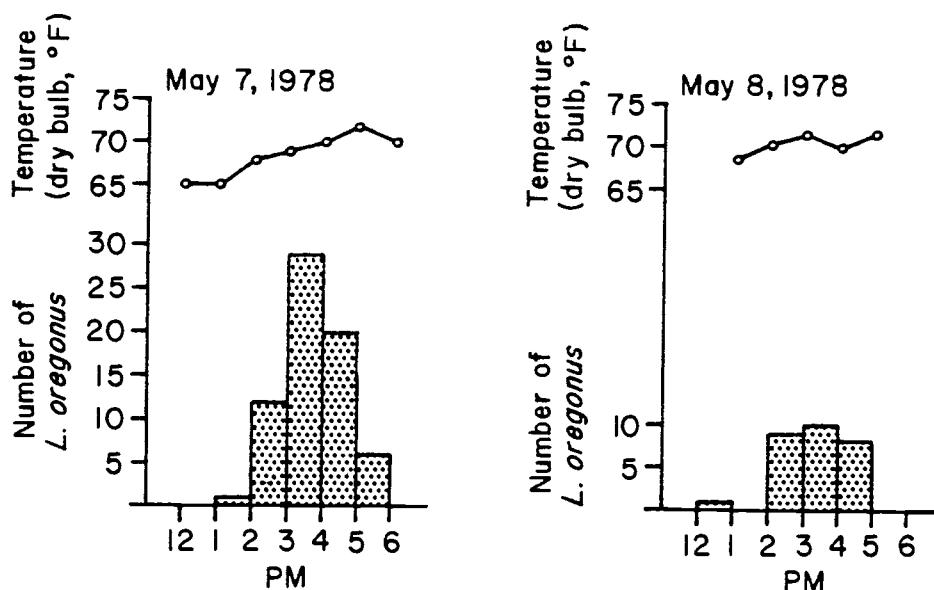


Fig. 2 Temporal distributions of *L. oregonus* attracted to a cage containing ash naturally infested with this species. (Day-light savings time)

both arms of the egg gallery are excavated by the same female.

Emergence

L. oregonus and *L. californicus* which attacked an ash (felled April 22, 1975) in May through early June produced progeny which were in late larval, pupal and callow adult stages by mid Aug. Emergence from log sections brought to the nursery on Aug. 11 began by Aug. 14, peaked in Sept. and continued as late as Oct. 19, 1975. Between Aug. 11 and Oct. 7 (when emergence was judged to be essentially over) 6988 *Leperisinus* adults emerged from 1800 galleries in the 6.38 m² surface area between the 24 cm diameter base and the point 12.71 m beyond the basal cut, where the diameter was about 11 cm. Of these, 5659 were *L. oregonus* (2882 males and 2777 females) and only 1329 were *L. californicus* (651 males and 678 females). Sex ratios were not significantly different from 1:1. This held for both species, tested separately. Fig. 3 shows that the yield of *L. californicus* (beetles per m²) was smaller than that of *L. oregonus* along the entire bole length. Fig. 4 shows that the *L. californicus* emergence also started and tapered off earlier. Possibly, it began before Aug. 11, 1975. The top, middle and bottom graphs in Fig. 5 show attack density (galleries per m²), yield in relation to

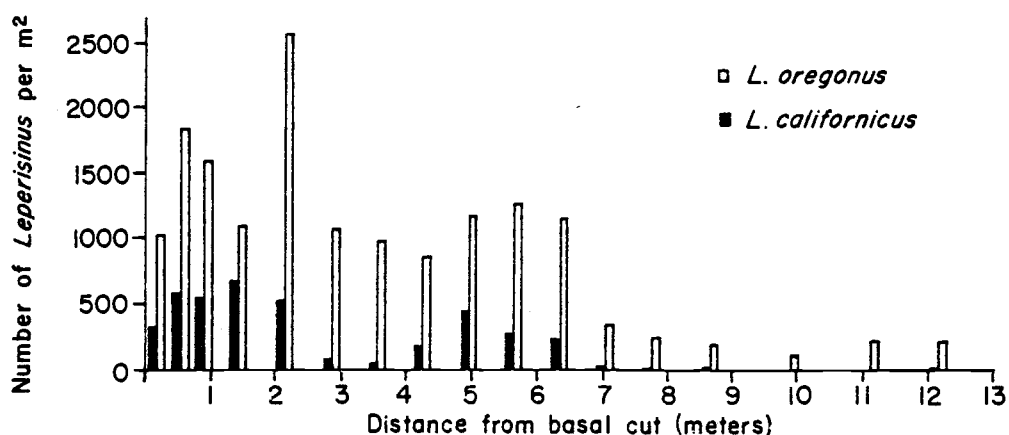


Fig. 3. Emergence of *L. oregonus* and *L. californicus* along the length of one felled *F. latifolia* between Aug. 11 and Oct. 7, 1975.

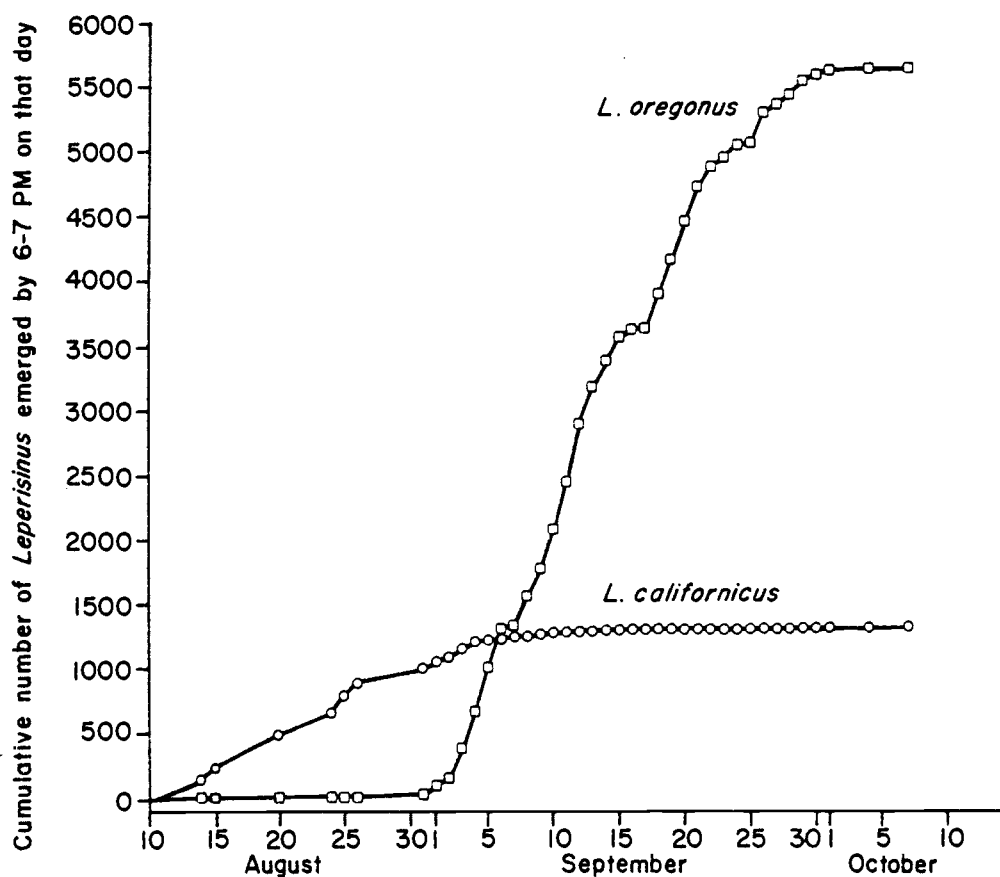


Fig. 4. Cumulative emergence of *L. oregonus* and *L. californicus* from one felled *F. latifolia* between Aug. 11 and Oct. 7, 1975.

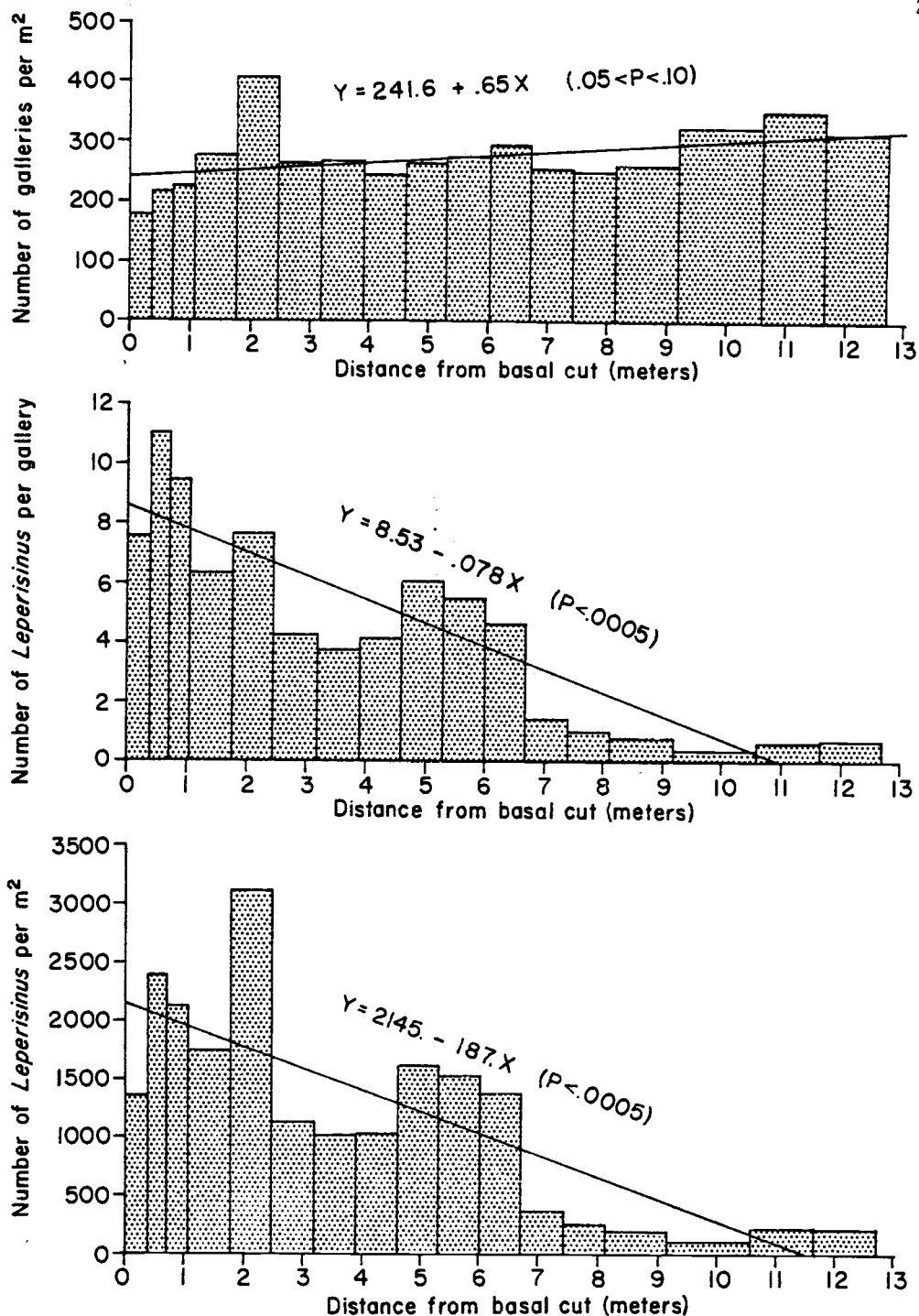


Fig. 5. Attack density and emergence of *Leperisinus* along the length of one felled *Fraxinus latifolia* between Aug. 11 and Oct. 7, 1975: galleries per unit surface area (top); beetles per gallery (middle); beetles per unit surface area (bottom).

attack (beetles per gallery) and yield in relation to surface area (beetles per m^2) along the bole length. The regression equations of these variables against distance from the basal cut indicate that attack density was fairly uniform ($R^2=.213$), but that a significant decrease occurred from the base towards the apex in brood production and/or survival as measured by beetles per gallery ($R^2=.789$) or beetles per m^2 ($R^2=.647$). Basal logs were observed to have long galleries with many egg niches and larval mines, whereas apical logs had short galleries with few niches and mines. Most apical sections were less moss-covered and also more exposed to direct sunlight simply because of where the tree fell. The highest emergence was from log sections 1.77 to 2.48 m from the basal cut. This was probably the area shaded by an overhanging bush, whose presence but not exact location was noted in the field while attacking beetles were being collected. In addition, apical logs have thin bark which is commonly considered easier for hymenopterous parasites to penetrate with their ovipositors. The large numbers of Coeloides scolytivorus which emerged in Aug. and Sept., 1975 and especially in June, 1976 came mainly from the apical logs. This braconid could have been an important mortality factor.

The relationship of L. oregonus emergence to temperature was examined. The 32 day period from Aug. 31 through Oct. 1, 1975 was rainless and included several hot spells (Fig. 7, upper graph) during which L. oregonus emergence fluctuated correspondingly (Fig. 7, lower graph). Daily L. oregonus emergence was strongly related to maximum daily temperature (Fig. 6) both with the full 32 days' data ($R^2=.645$) and without three noticeable outliers ($R^2=.869$). These outliers were near the end of Sept., when small numbers of L. oregonus ready to emerge did so mainly on the first days of the last two warm spells. Consequently, few beetles were left to emerge on the following days, despite continued high temperatures. Goeden and Norris (1964) reported that emergence of Scolytus quadrispinosus (the hickory bark beetle) fluctuated with maximum daily temperature and was negligible below 21-23°C. The threshold for L. oregonus emergence is probably not far below 69°F (20.6°C), the lowest maximum daily temperature, which occurred twice, between Aug. 31 and Oct.

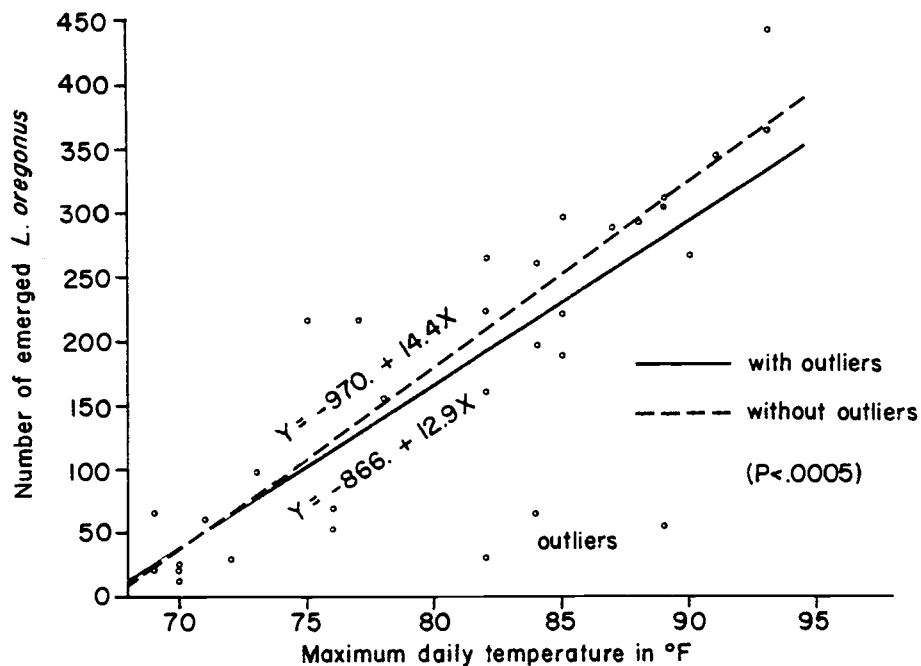


Fig. 6. Relationship of *L. oregonus* emergence to maximum daily temperature between Aug. 31 and Oct. 1, 1975.

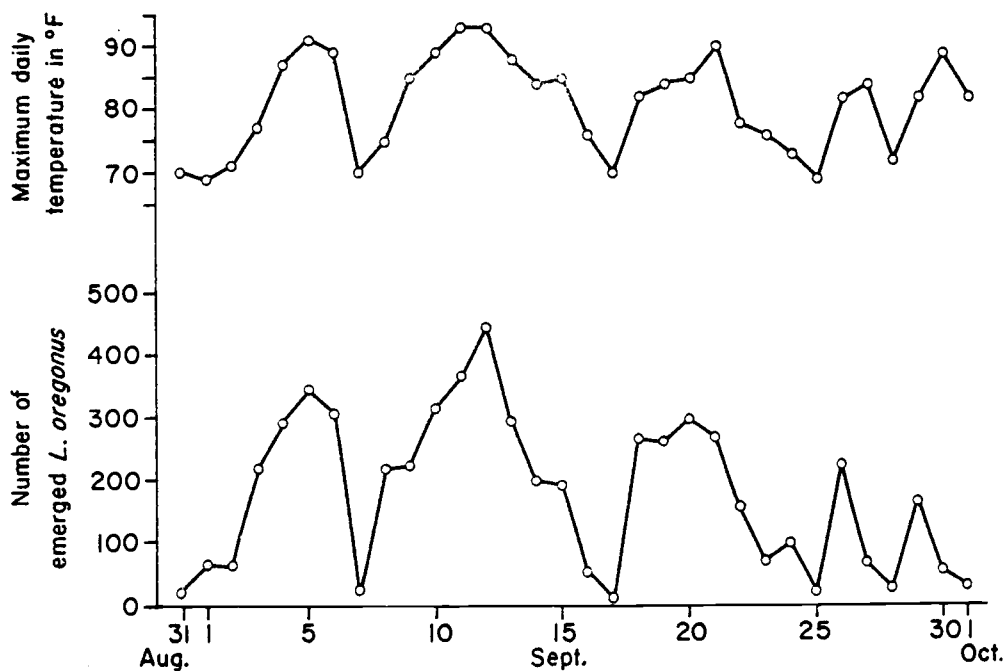


Fig. 7. Hot spells accompanied by waves of *L. oregonus* emergence between Aug. 31 and Oct. 1, 1975.

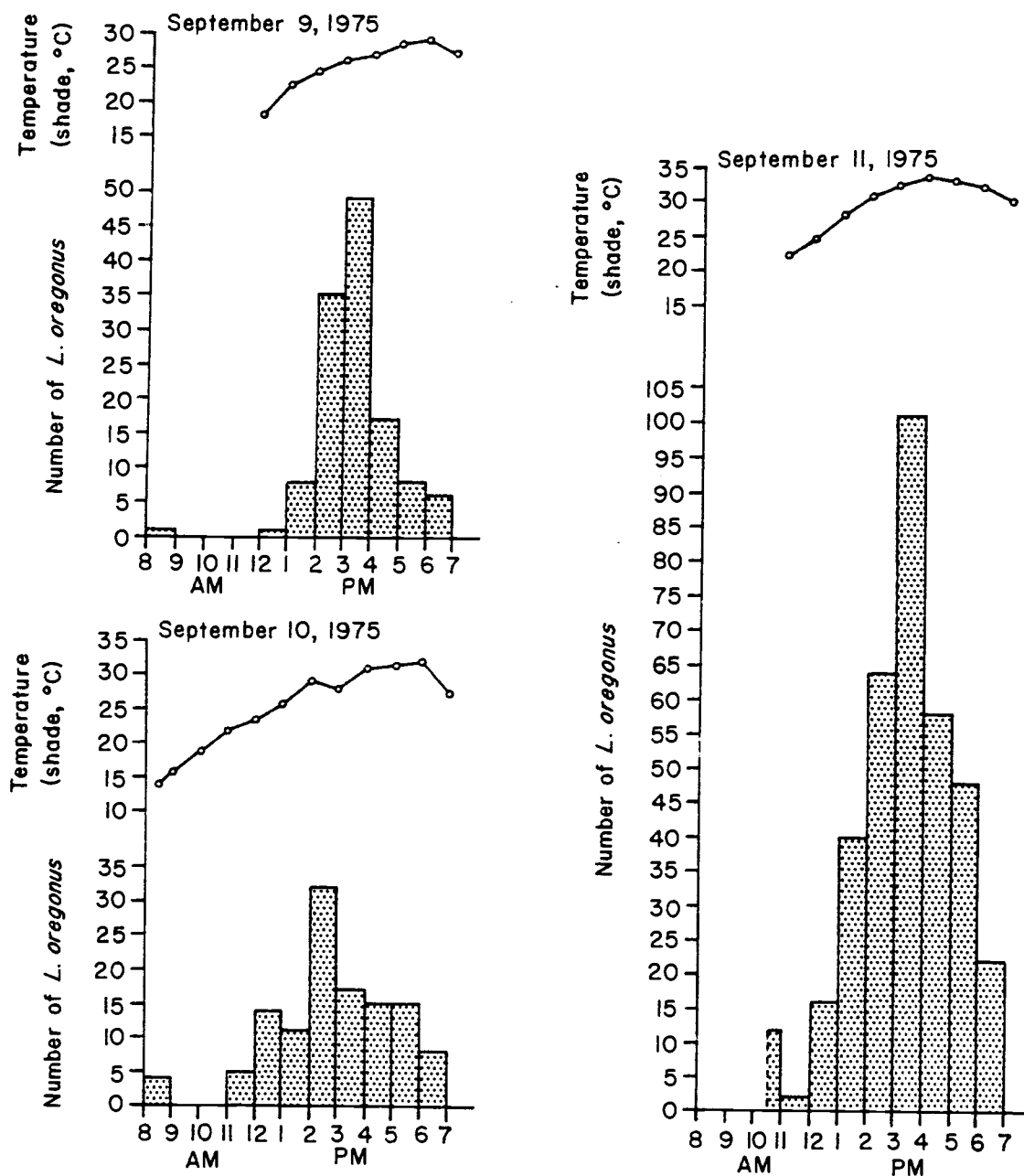


Fig. 8. Shade temperature and hourly emergence of *L. oregonus* on three days in late Summer, 1975. The same numbers of log sections were not used on all three days. (Daylight savings time)

1, 1975. The coolest days, with maximum daily temperature below 74°F (23.1°C), comprised 25 percent of the days but accounted for only six percent of the total emergence (from the one ash tree) during this period. Goeden and Norris (1964) confirmed their threshold for S. quadrispinosus using hourly collections. Few L. oregonus emerged before 11 A.M. to noon, when temperatures were 18-22°C, on the three days when hourly collections were made (Fig. 8). The regression of hourly L. oregonus emergence on shade temperature at the end of each hour was significant ($P < .005$, $R^2 = .778$, hourly emergence = $-253.6 + 9.73(\text{hourly } ^\circ\text{C})$) only on Sept. 11, a very hot day when the greatest number of logs was used. Numbers peaked in midafternoon and dropped off towards sunset, despite continued high temperatures. Hourly emergence of L. oregonus was not as closely related to temperature as was its daily emergence.

Maturation feeding observations

Both L. oregonus and L. californicus are sexually immature when they emerge from brood logs. Of about 127 L. oregonus females which were dissected after emerging between Aug. 14 and Sept. 12, 1975, most had small germaria, no follicle differentiation and, when checked, small and usually white colleterial glands. Only six were in intermediate stages of development, with swollen germaria and sometimes one distinctly enlarged egg per ovariole. Only two appeared mature. The colleterial glands of some of these more developed females were yellow, and they may have been reemerged parents. Of 40 L. californicus females which were dissected after emerging on Aug. 14-26, 1975, most were immature, and only two had slight egg development. All of the approximately 111 L. oregonus males which were dissected after emerging on Sept. 9-12, 1975 had tiny seminal vesicles but moderately sized testes. The five L. californicus males dissected from the Aug. 26, 1975 emergence had small seminal vesicles. No special note was made, but immature males also had very thin accessory glands. Thus both sexes of these Leperisinus spp. are immature upon emergence as young adults.

In contrast, attacking L. oregonus and L. californicus are sexually mature. The thin, elongated area just below the swollen germarium, when

left in 70 percent ethanol for about an hour, can be seen to have very small follicles which are not visible in fresh dissections. Below this area, several distinctly enlarged and rounded eggs can be counted in each of the four ovarioles of mature females. Thirteen L. oregonus females (eight paired, five unpaired) and nineteen L. californicus females (17 paired, two unpaired) were excised from breeding galleries and had two to four distinct eggs per ovariole. Eggs were large only at the bases of the ovarioles and in the oviducts. Size and color of colleterial glands varied from small to large and from white to yellow. Thirty-five L. californicus females trapped to cages containing infested ash logs had two to five distinct eggs per ovariole. Their colleterial glands varied from white to yellow, with a few having one of each color. The five L. oregonus males (four paired, one unpaired) excised from galleries were mature on the basis of enlarged, white seminal vesicles and accessory glands as well as enlarged, white and yellow testes. Sixteen L. californicus males trapped to cages containing infested ash logs had enlarged or partially enlarged seminal vesicles and accessory glands. Thus substantial development of male as well as female reproductive systems takes place in adults of both Leperisinus spp. between emergence and breeding attack.

Between emergence and breeding attack, Leperisinus adults are difficult to locate. Underhill's (1951) statements suggest that he found quite a few overwintering L. oregonus, but he made no mention of whether they were sexually mature. My field observations of Leperisinus in non-breeding galleries were limited. Several L. oregonus males and females were found unexpectedly in the greenhouse inside cages containing logs cut April 15, 1975 and brought in from the field immediately. One L. oregonus female was found in a short bark burrow facing the apical end of a 14 cm log cut Feb. 27, 1978. She had enlarged germaria and about one distinct egg per ovariole. Examination of several other logs cut that day revealed only a dead L. oregonus male in one burrow and some old, abandoned burrows. Fifteen L. oregonus (seven females, eight males) were found on Aug. 26-27, 1975 in individual 4-9 mm long bark burrows in ash logs from a tree felled Aug. 16, 1975, wrapped tightly with sheets and tape to prevent breeding attack on Aug. 16 and 18

during cool, rainy weather and bucked Aug. 26. These beetles probably were in the living tree when it was felled, since no L. californicus had bypassed the wrapping to attack, despite the fact that the latter species was flying then. However, at least the females in this group of L. oregonus were mature, with two to four eggs per ovariole and variable colleterial glands. They may have been reemerged parents. An extensive search for overwintering L. oregonus was not undertaken, since their density appeared to be zero to two per 60-90 cm long log. No abnormal tissue growth around overwintering burrows was noted on ash in Oregon by either Underhill (1951) or myself.

Only eight living L. californicus were found in non-breeding galleries. A female with at least one distinct egg per ovariole was found in a 2.5 mm long twig crotch burrow in an ash sprout on March 29, 1975. An apparently senescent female was found in a twig crotch burrow on April 30, 1975, in an ash felled April 15. A male was found barely scoring sapwood alongside an axillary bud of a living ash on July 7, 1975. A male boring in a succulent leaf axil of a living ash was found on Aug. 4, 1975. An L. californicus, lost before sexing, was found in a twig crotch burrow at least 10 mm long in ash tops as soon as two trees were felled on Feb. 27, 1978. On Feb. 28, these two crowns were thoroughly searched but only three beetles were found: a female just starting a twig crotch burrow, a female in a terminal bud, and a male in a burrow along the underside of a twig junction. Both females were partly mature, with enlarged germaria, one distinct egg per ovariole, and small white colleterial glands. The male appeared old, with enlarged but stiff organs containing hard material. Thus, both immature and (probably) reemerged L. californicus of both sexes were found in twig crotches, buds and leaf axils. Some dead L. californicus were found in twig crotch burrows, and abandoned twig burrows were fairly common.

Leperisinus is not the only scolytid genus with species known to undergo maturation feeding after emergence from brood logs rather than in bark surrounding pupal chambers. Others include Pseudohylesinus nebulosus in Douglas fir (Stoszek and Rudinsky, 1967), Hylurgopinus

rufipes in elm (Kaston, 1939), Scolytus quadrispinosus in hickory (Goeden and Norris, 1964) and Conophthorus coniperda in white pine (Henson, 1961). A "close relative" of Leperisinus spp., Hylesinus (= Chaetoptelius) vestitus, causes economic damage to terminal and floral buds of pistachio, but no mention was made of maturation (Yaman, 1969). The twig crotch boring habit of Scolytus multistriatus, by which means it transmits Dutch elm disease, is not obligatory but "provides nutrients for survival and sexual maturation if weakened or dying elms suitable for beetle oviposition are unavailable" (Baker and Norris, 1968). The feeding of a Leperisinus sp. in quarter-inch burrows at buds or in axils of Fraxinus twigs at Stanford Univ. (Herbert, 1920) was soon followed by Doane's (1923) report of F. americana mortality due to L. californicus on that campus.

Maturation feeding experiments

Efforts to obtain sexually mature Leperisinus for behavioral tests, by feeding them on ash in confinement, were time consuming and only partially successful but did yield some biological information.

L. oregonus which emerged and which were caged on living ash saplings or branches at Jackson Place in late Sept. and early Oct., 1975 were excised and dissected between mid March and mid June, 1976. Those excised in March showed little or no development. On April 11, about half (18 of 40) females had one distinct egg per ovariole while the others (13 of 40) found intact had none. Males showed little seminal vesicle enlargement. On April 25, about half (10 of 21) of the females found alive had two distinct eggs per ovariole while the other 11 had one. On May 3, only six females were dissected, and each had one to two distinct eggs per ovariole. On June 14, most beetles were used for behavioral observations and audiorecordings after being excised, but the two females dissected had two to three eggs per ovariole, and the two males dissected had partially enlarged seminal vesicles. This last condition was considered minimal maturity. The apparently slow development of these experimentally overwintered L. oregonus may have been due to location of the sleeve-cages below two meters rather than in the more

sunlit crowns. Additional shading of bole segments in white cotton sleeves may have also lowered the temperature. Also, between one-fifth (April 11) and one-third (June 14) of the beetles escaped, possibly the more mature individuals. Another third of the group examined in June was dead. The most consistent result was that burrows were constructed in living bark by individual L. oregonus, generally faced upward, and did not score sapwood.

When logs containing emerging young adults, mainly L. californicus, were left in the greenhouse with cut ash sprouts placed in water, they readily entered the twigs. They left 126 burrows, most (84 percent) starting at twig crotches and others either at nodes or, rarely, at interspaces. These were 1.5-37. mm long ($\bar{x}=9.4$), 1.-5. mm in diameter ($\bar{x}=2.2$) in 2.5-15. mm thick twigs. They reached either the sapwood (56 percent) or the pith (44 percent). Most were abandoned (87 percent) by the time they were examined, and samples examined three to five weeks after the experiment began were only 52 percent occupied (17 of 33). Each beetle was in a separate burrow. The nine females had little or no egg development, but their maturation probably lagged behind that of females which had already left the twig burrows. Most burrows were clean (78 percent), but the others had sap, mold, both or frass. Some of the attacked sprouts dried out and died, while others exuded sap which filled the burrows and eventually began to leaf. The beetles' persistent choice of twig crotches or nodes may have been influenced by localized host tissue conditions. It may be because the beetle can brace itself against a branch or bud when starting its excavation in this location.

In another series of experiments, two generations of L. californicus were produced in the greenhouse. The parent generation emerged from brood logs in a white drapery cloth cage between late Jan. and late March. Only two were found in the litter and soil, but they entered the ash sprouts and 126 feeding scars or burrows were counted (but not measured) when the cage was finally emptied. On April 3, L. californicus (5 males alone, 5 females alone, 4 pairs) and a few L. oregonus (2 in irregular galleries) were found in one of the thin-barked logs. By May 12, pupae, callow adults and hardened adults were in pupal chambers in these logs. Between May 13 and July 4, 1975 over 1760 L. californicus

were collected from this cage, probably mostly the F-1 generation. They were stored in the refrigerator and, on July 17, over 600 were placed, sexes separate, on cut twigs in six 38 cm³ galvanized metal boxes with light jars. After 12 days, a few females had slight egg development. After 20 days, some females had two to three distinct eggs per ovariole. On Aug. 28, about 90 males and 120 females were taken from the light jars and placed in a small cloth-lined cage with logs cut Aug. 26 after ten days' transpiration. They produced about 40 piles of frass by the next day and began to pair and oviposit before Sept. 8. The logs were watered occasionally, and the F-2 generation emerged from them and was collected between Nov. 16, 1975 and Jan. 30, 1976. To ascertain that they were progeny, 48 of these L. californicus were dissected in late Nov. and both sexes found to be immature. This demonstrates that L. californicus can reproduce in the greenhouse under a variety of conditions for at least two generations, as long as it is provided with ash that is not dried out. The problem of obtaining uniformly mature beetles by allowing them to feed but removing them before females begin breeding galleries, was not solved.

Hymenopterous parasites or associates of Leperisinus

Seven species of Hymenoptera were obtained in association with ash logs infested by L. oregonus, L. californicus and a cerambycid, Neoclytus conjunctus LeC. Braconids were Coeloides scolytivorus (Cresson) (over 270), Spathius benefactor Matthews (94) and Atanycolus malii Schenefelt (11). Among C. scolytivorus, males predominated. Among S. benefactor, females predominated. A. malii is not considered a scolytid parasite (Marsh, letter, Jan. 5, 1978), and the only female specimen I collected was ovipositing in an ash log above a large larva with cylindrical body and coarse frass typical of cerambycids. Pteromalids were Cheiropachus quadrum (Fabricius) (51) and Habrocytus sp. (39). Eurytomids were Eurytoma sp. (2) and Harmolita sp. (2).

Table III shows the various situations in which most of these specimens were collected.

TABLE III. HYMENOPTERA COLLECTED IN ASSOCIATION WITH LOGS INFESTED BY L. OREGONUS, L. CALIFORNICUS AND NEOCLYTUS CONJUNTUS

Species	No. of specimens in each situation						
	L-R	G-E1	G-E2	N-E	Cg	Ld	G Ov
<u>Coeloides scolytivorus</u> (Cresson)	1	5+	0	234+	0	0	0 0
<u>Spathius benefactor</u> Matthews	0	17+	4	25	26+	0	2 0
<u>Atanycolus malii</u> Schenefelt	1	5	0	4	0	0	0 1
<u>Cheiopachus quadrum</u> (Fabricius)	16	0	0	24	9	2	0 0
<u>Habrocytus</u> sp.	0	12	0	27	0	0	0 0
<u>Eurytoma</u> sp.	0	0	0	2	0	0	0 0
<u>Harmolita</u> sp.	0	0	0	0	2	0	0 0

Abbreviations: L-R, laboratory-reared after being collected in Jan., 1975 as immatures from among Leperisinus gallery systems in tops of ash felled and infested in 1974; G-E1, greenhouse-emerged from infested logs of the same 1974 ash; G-E2, greenhouse-emerged from ash logs infested in 1975; N-E, nursery-emerged from logs of an ash felled April 22, 1975 or from logs collected from the same site that year; Cg, landed on cages containing ash logs (in the field), most of which were naturally infested with and attractive to L. californicus adults; Ld, landed on ash during Spring attack in 1975; G, general collecting in ash stand; Ov, taken while ovipositing on a cerambycid(?) larva. + means that an unknown number in this category were retained by the National Museum or II&BIII of the USDA.

Other reports of these parasites on Leperisinus spp. include Coeloides scolytivorus on L. aculeatus (Fiske, 1907; Hoffmann, 1938 from New Jersey; Beal and Massey, 1945 from North Carolina), of which it is a primary parasite (Hoffman, 1938), and Cheiopachys¹ quadrum on L. fraxini and Scolytus laevis in Norway (Pettersen, 1976). Congeneric parasite records include Cheiopachus colon L. and Eurytoma crassineura Ashm. on our Oregon Leperisinus (Underhill, 1951), E. crassineura from ash infested with L. criddlei (McKnight and Aarhus, 1973), Spathius canadensis and a Eurytoma sp. from L. aculeatus or C. scolytivorus (Hoffmann, 1938) and a Eurytoma sp. associated with L. aculeatus (Beal and Massey, 1945). In Europe, several Coeloides, Spathius, Cheiopachys and Eurytoma spp. are parasites or hyperparasites of L. fraxini (Escherich, 1923; Russo, 1926 and 1932, Nunberg, 1930; Del Guercio, 1931;

¹ Incorrect spelling of Cheiopachus (Peck, 1963), used in Europe.

Sitowski, 1933; Sokanowsky, 1936; Chararas, 1958; Jamnický, 1959). Based on the literature and on high numbers obtained emerging from from the ash infested mainly with L. oregonus but also L. californicus, I would consider C. scolytivorus a primary parasite of one or both species. Since S. benefactor was attracted to the same cages with infested ash as was L. californicus in Aug., 1975 and no C. scolytivorus were collected at this time, this Spathius sp. may also be a primary parasite.

Morphology of the acoustic organs

Introduction

The acoustic organs of L. oregonus and L. californicus are qualitatively similar to each other. The male pars stridens (Plate I, A-F) consists of two files of fine, generally parallel but sometimes forking ridges on the inner surfaces of the elytral tips. The ridges appear transverse on the left elytron and diagonal on the right. In L. californicus, additional long but faint ridges run along the posterior elytral edges, behind a hard ridge which separates them from the file. In L. oregonus, this area is broken into irregular, polygonal plates. In L. californicus, the ridges are more elevated near the midline than laterally. This difference is less apparent under the light microscope (in bright field) than in the SEM. Even fainter lateral extensions of the ridges, in L. californicus, were not considered part of the file width and probably correspond to the "Übergangsstruktur" (transitional structure) noted by Marcu (1931) in Hylesinus crenatus and H. oleiperda but not in L. fraxini or L. orni. Female files (not shown) are qualitatively similar to those of males. File ridges, in the central part (Plate II, A-H), appear sharp on both sides and in both sexes. However, one L. californicus female SEM specimen had flattened ridges (not shown).

The plectrum is a pair of scrapers on the posterior edge of the male's seventh tergite (Plate III, A-B). Each consists of a process and a seta (Plate III, C-E). Scrapers are absent in females (Plate

Scanning electron micrographs illustrating the stridulatory apparatus
of Leperisinus oregonus Blackman and L. californicus Swaine

- Plate I. The pars stridens or elytral files. L. oregonus male (A) left file, (B) part of right file, (C) winglock and medial portions of both files, taken with wings nearly locked; L. californicus male (D) left file, (E) part of right file, turned so posterior end is to the left, (F) winglock and medial portions of both files, taken with wings nearly locked. Posterior end is toward top of figure, except in (E). Legend: sm, sutural margin of elytron; wl, winglock area (scaly gap between left elytron's sutural margin and left file's medial edge).
- PLATE II. Close-up views of file ridges. L. oregonus male (A) left, (B) right; L. oregonus female (C) left, (D) right; L. californicus male (E) left, (F) right; L. californicus female (G) left, (H) right.
- PLATE III. The plectrum in males and its absence in females. (A) L. oregonus male, plectrum on posterior edge of seventh abdominal tergite; (B) L. californicus male, plectrum on posterior edge of seventh abdominal tergite; (C) and (D) L. oregonus male, left scraper at two different angles; (E) L. californicus male, left scraper; (F) L. oregonus female, posterior abdominal tergites with plectrum absent; (G) L. californicus female, posterior abdominal tergites with plectrum absent. Legend: ant, anterior edge of photo; pl, plectrum; pm, posterior margin of abdomen; pr, process of scraper; sa, setose area (not part of stridulatory apparatus); scl, sclerotized band at posterior margin of seventh tergite; se, seta of scraper.

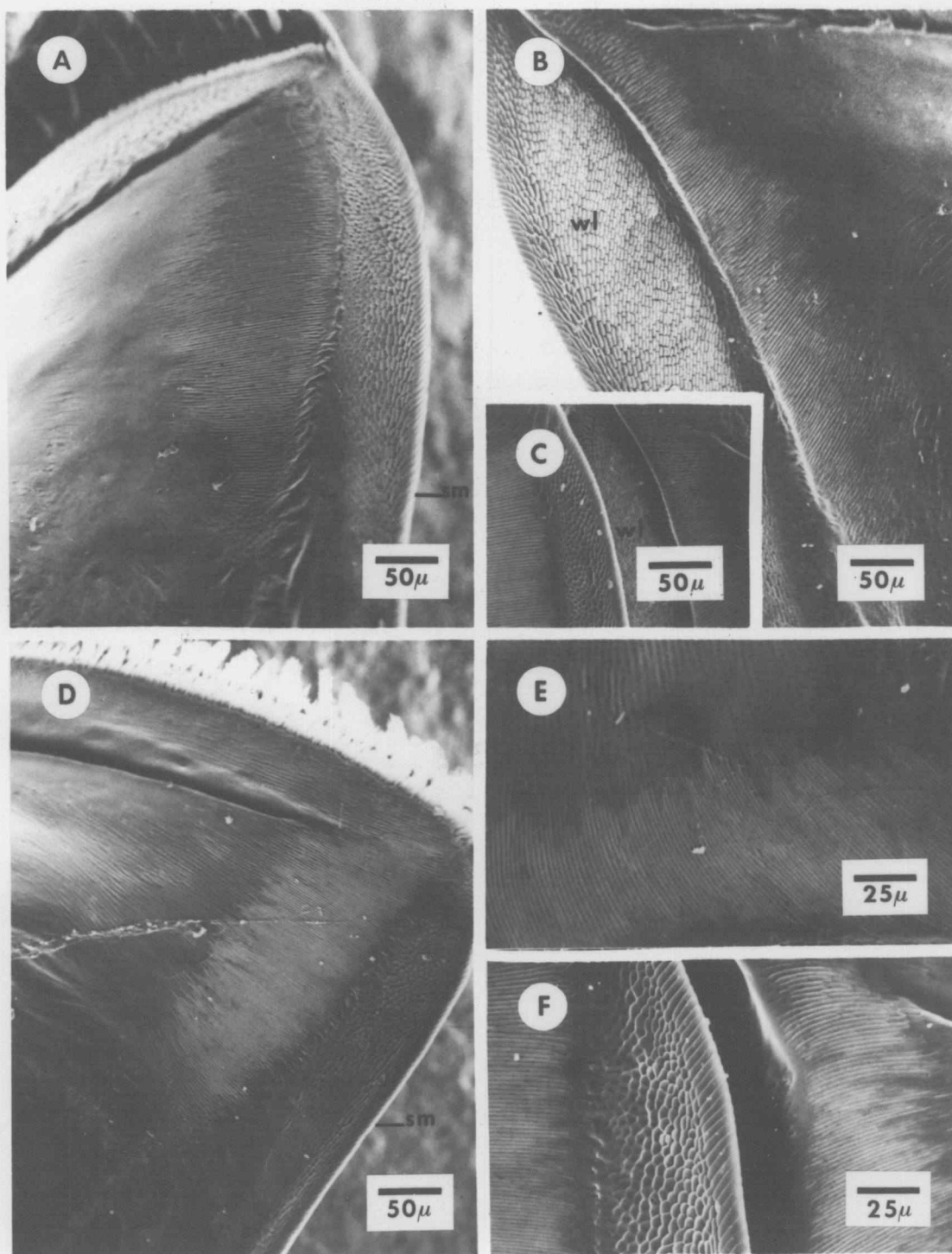


Plate I

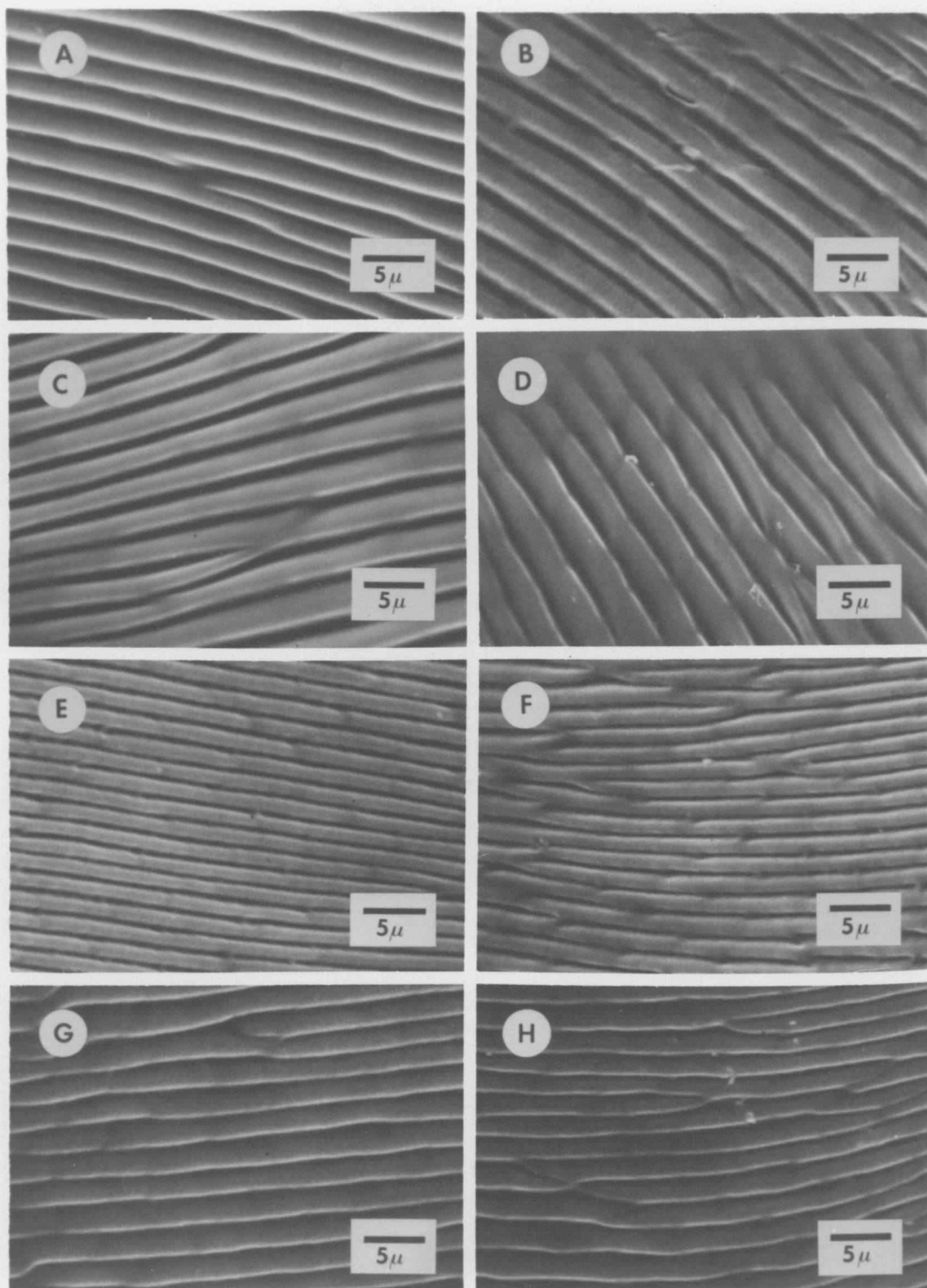


Plate II

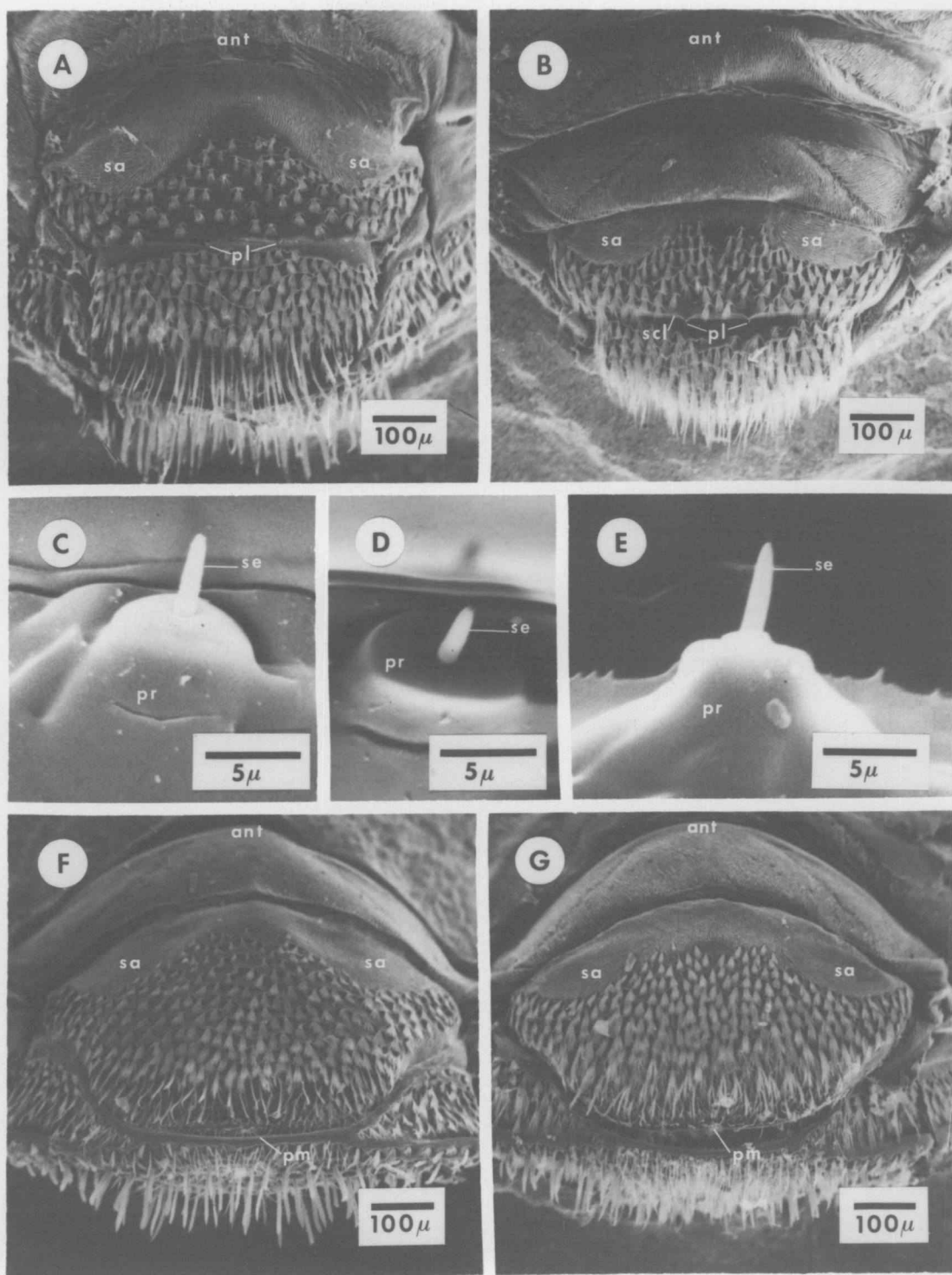


Plate III

III, F-G), whose posterior abdominal edges are less hairy than in males.

Descriptive statistics for left files, scrapers and right files are presented in Tables IV, V and VI, respectively. The four groups of beetles, male or female L. oregonus or L. californicus, will be referred to as "species-sex" groups.

Differences among species-sex groups

All but one variable, the gap between the left elytron's sutural margin and the left file's medial edge, showed significant differences ($P < .0005$) among the four species sex groups. No single variable could separate them completely. Some revealed species differences, some sexual dimorphism, and some both. Others separated out one or two groups.

L. oregonus males had scrapers about 16μ further apart than L. californicus males ($P < .001$).

L. oregonus had longer elytra than L. californicus ($P < .0005$). Females had longer elytra than males ($P < .0005$). There was considerable overlap among groups.

Sexual dimorphism in the number of file ridges, on both right and left sides, was significant ($P < .0005$) and marked, with males having more ridges than females. There was no overlap between sexes in left file ridge number, although the maximum for females approached the minimum for males, and little overlap (two out of 104 beetles) in right file ridge number. There was no species difference in these variables.

The species difference in file length, on both right and left sides, was significant ($P < .0005$) and marked, with L. oregonus having longer files than L. californicus. Males had longer files than females in L. oregonus but not in L. californicus, so sexual dimorphism could not be claimed, in general, for file length.

Fig. 9 shows that left file ridge number and left file length together could separate males of the two Leperisinus spp. completely, and that ridges were denser in L. californicus males, with no overlap.

File width separated the females of the two Leperisinus spp. L.

TABLE IV. MORPHOLOGY OF LEPERISINUS SPP. LEFT FILES

Structure and measurement	Sex	L. oregonus (n=26 per sex)					L. californicus (n=26 per sex)				
		Mean	gr	Range	S.E.	C.V.	Mean	gr	Range	S.E.	C.V.
Outside elytral length (μ) (crenulations to tip)	M	2422.	bc	2194.-2597.	22.96	4.8	2244.	a	1928.-2424.	22.22	5.1
	F	2539.	c	2187.-2978.	40.92	8.2	2328.	ab	2108.-2511.	19.63	4.3
Inside elytral length (μ) (muscle attachment to tip)	M	2027.	ab	1842.-2230.	20.16	5.1	1927.	a	1705.-2209.	21.03	5.6
	F	2136.	b	1849.-2518.	34.93	8.3	2005.	a	1813.-2115.	16.18	4.1
Number of file ridges	M	135.9	b	118-162	2.431	9.1	142.2	b	118-167	2.489	8.9
	F	98.8	a	77-115	1.703	8.8	88.7	a	68-108	2.101	12.1
Maximum file length (μ)	M	439.2	c	358.9-522.9	8.824	10.2	300.5	a	236.2-362.0	6.129	10.4
	F	383.6	b	285.1-455.3	7.941	10.6	281.5	a	228.2-322.7	4.565	8.3
Maximum file width (μ)	M	137.5	b	119.1-155.8	1.884	7.0	133.2	b	117.3-156.0	1.905	7.3
	F	107.8	a	83.1-136.9	2.729	12.9	142.7	b	120.0-164.2	1.911	6.8
Gap between sutural margin and file's medial edge (μ)	M	76.9		65.8- 90.9	1.163	7.7	74.4		65.3- 88.2	1.158	7.9
	F	79.4		62.9- 91.3	1.509	9.7	76.8		67.6- 91.8	1.292	8.6
File ridge spacing (μ) (mean of 30 central ridges)	M	2.974	b	2.659-3.274	.0376	6.5	1.925	a	1.637-2.237	.0310	8.2
	F	3.509	c	3.111-3.941	.0408	5.9	2.804	b	2.415-3.393	.0506	9.2
File ridge density per mm (ratio of no. to length)	M	310.2	b	272.7-337.3	3.305	5.4	474.7	c	417.1-531.1	6.050	6.5
	F	258.4	a	231.4-293.8	2.899	5.7	315.1	b	266.1-390.2	5.485	8.9

Abbreviations: C.V., coefficient of variation (percent); gr, groupings using Scheffé's multiple comparison test at a probability level of .01, if one-way ANOVA revealed significant differences among the four species-sex groups for the variable within the solid lines; S.E., standard error of the mean

TABLE V. MORPHOLOGY OF LEPERISINUS SPP. MALE SCRAPERS

Measurement	L. oregonus (n=26)					L. californicus (n=26)				
	Mean	gr	Range	S.E.	C.V.	Mean	gr	Range	S.E.	C.V.
Distance between processes (μ) from bases of setae	127.7	b	108.2-144.5	1.944	7.8	111.4	a	91.1-141.0	2.357	10.8

Abbreviations: C.V., coefficient of variation (percent); gr, grouping using unpaired Student's t-test; S.E., standard error of the mean

TABLE VI. MORPHOLOGY OF LEPERISINUS SPP. RIGHT FILES

Structure and measurement	Sex	L. oregonus (n=26 per sex)					L. californicus (n=26 per sex)				
		Mean	gr	Range	S.E.	C.V.	Mean	gr	Range	S.E.	C.V.
Outside elytral length (μ) (crenulations to tip)	M	2429. bc		2216.-2604.	22.66	4.8	2244. a		1942.-2410.	22.14	5.0
	F	2544. c		2209.-2957.	40.88	8.2	2333. ab		2137.-2489.	19.45	4.3
Inside elytral length (μ) (muscle attachment to tip)	M	2032. ab		1871.-2252.	20.57	5.2	1914. a		1719.-2180.	21.35	5.7
	F	2137. b		1856.-2489.	35.80	8.5	2014. a		1827.-2137.	16.92	4.3
Number of file ridges	M	130.0 b		105-149	2.258	8.9	130.6 b		110-160	2.077	8.1
	F	86.3 a		63-106	1.929	11.4	83.8 a		71-94	1.218	7.4
Maximum file length (μ)	M	464.4 c		352.7-538.0	10.03	11.0	346.4 a		274.0-423.6	8.40	12.4
	F	417.9 b		293.3-492.7	9.58	11.7	324.4 a		287.1-366.9	4.64	7.3
Maximum file width perpen- dicular to median axis (μ)	M	84.4 b		66.4- 93.6	1.39	8.4	88.9 b		75.6-109.3	1.91	10.9
	F	70.1 a		47.3- 91.3	2.23	16.2	100.7 c		78.0-119.1	2.05	10.4
Maximum file width paral- lel to ridges (μ)	M	105.0 ab		80.7-156.0	3.22	15.7	111.4 b		93.8-151.3	2.45	11.2
	F	93.6 a		62.0-128.0	3.21	17.5	126.9 c		107.8-159.1	2.65	10.6
File ridge spacing (μ) (mean of 30 central ridges)	M	3.056 c		2.756-3.289	.0317	5.3	1.923 a		1.681-2.170	.0280	7.4
	F	3.572 d		3.089-4.052	.0491	7.0	2.670 b		2.230-3.111	.0525	10.0
File ridge density per mm (ratio of no. to length)	M	281.4 c		246.6-334.6	4.221	7.6	380.0 d		306.9-444.7	6.711	9.0
	F	207.2 a		180.4-229.3	2.621	6.5	258.8 b		235.1-299.8	3.455	6.8

Abbreviations: C.V., coefficient of variation (percent); gr, groupings using Scheffé's multiple comparison test at a probability level of .01, if one-way ANOVA revealed significant differences among the four species-sex groups for the variable within the solid lines; S.E., standard error of the mean.

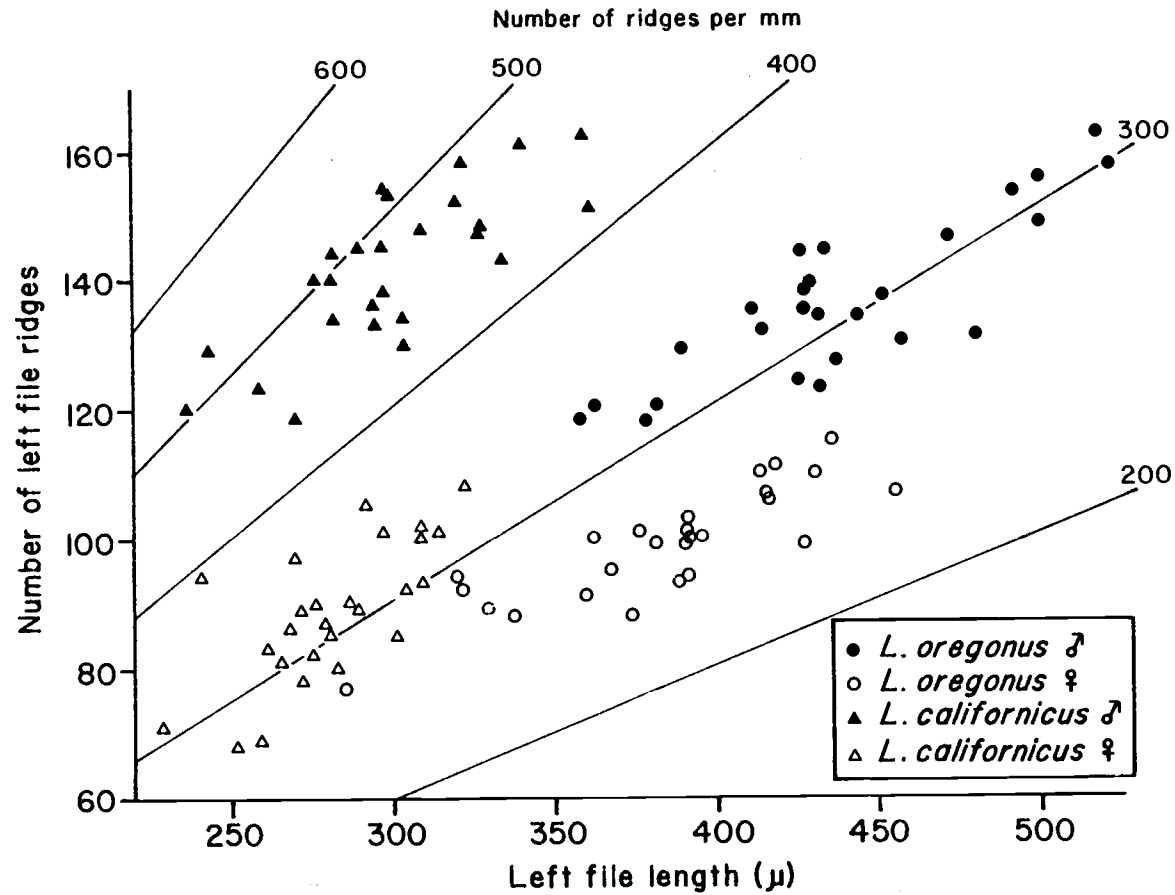


Fig. 9. Separation of male and female *L. oregonus* and *L. californicus* left files using number of ridges and maximum length, with ridge density (a ratio) indicated by diagonal lines. Each point represents measurements on one beetle.

oregonus females had narrower left files than the other three species-sex groups. Right files, measured perpendicular to the median axis, were narrowest in L. oregonus females and widest in L. californicus females, with no difference between the intermediate, male groups. Right files, measured parallel to the ridges, followed a similar pattern, except that L. oregonus males and females did not differ. In these three width variables, strong interactions ($P < .0005$) prevented generalizations about species or sex differences.

Ridge spacing, measured on 30 central ridges, showed significant species differences ($P < .0005$) and sexual dimorphism ($P < .0005$), despite significant interactions ($P < .0005$ on the left, $P < .01$ on the right). L. californicus males had the most closely spaced ridges and L. oregonus females had the most widely spaced ridges, with the other two groups intermediate. Ridge density, a ratio of file ridge number to file length, showed significant but less marked differences, with a strong interaction that overruled species and sex differences on the left side. The most important result was that L. oregonus males and L. californicus males did not overlap in central ridge spacing of either file or in overall ridge density of the left file.

To see how effective the variables were in combination, the following five variables were used in one-way and two-way multivariate analyses of variance (MANOVAs):

- outside elytral length (μ)
- number of file ridges
- maximum file length (μ)
- maximum file width (μ) (perpendicular to median axis)
- file ridge spacing (μ) (mean of 30 central ridges)

Left and right files were analyzed separately. Except where specified, statements apply to both sides.

The four species-sex groups differed significantly ($P < .0005$) in the full five-variable model but also in all four-, three- and two-variable models. The best reduced models are indicated in Tables VII and VIII, for left and right sides, respectively. When the first and second discriminant functions of the full model are plotted together, the species-sex groups separate into four distinct clusters of 26 points each. Fig. 10 shows this separation in left side data, with each point corresponding

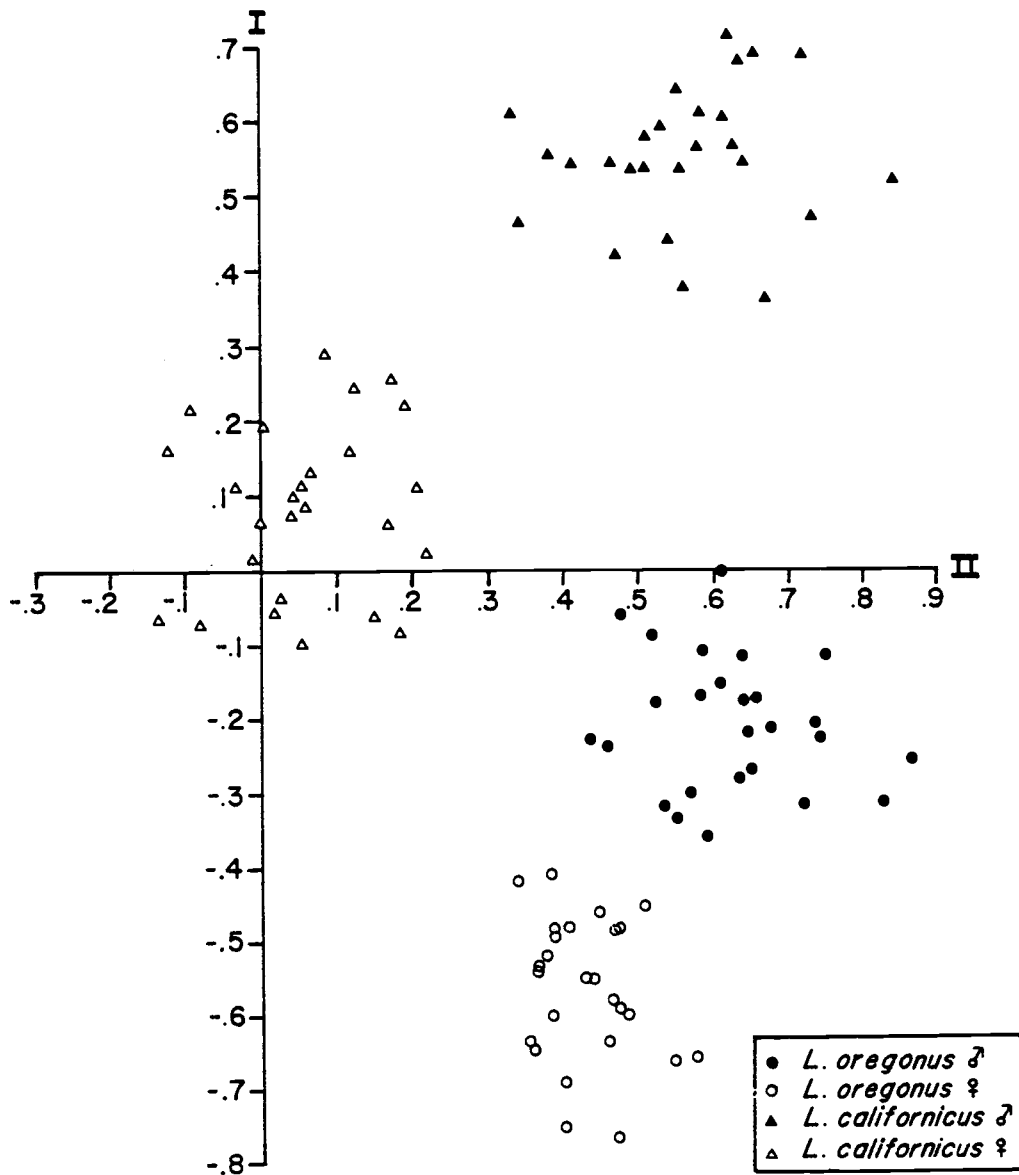
TABLE VII. RESULTS OF ONE-WAY MANOVAs ON LEFT-SIDE MEASUREMENTS

Number of variables (p)	Parameters included in the best p-variable model	Correlations of variables with discriminant functions			Percent of inter- group variation accounted for by discrim. function			Eta- squared (1 - Δ)
		1st	2nd	3rd	1st	2nd	3rd	
5	elytral length	-.63	.07	-.09	71.4	20.3	8.3	.997
	no. of ridges	.44	.85	.19				
	file length	-.61	.62	.37				
	file width	.50	-.21	.71				
	ridge spacing	-.95	-.17	.03				
4	elytral length	-.63	.11	-.09	69.0	21.7	9.3	.997
	no. of ridges	.49	.83	.18				
	file length	-.57	.67	.36				
	file width	.49	-.24	.71				
3	no. of ridges	.49	.81	.33	73.2	22.6	4.2	.994
	file length	-.57	.63	.52				
	file width	.49	-.29	.82				
2	no. of ridges	.66	.75	---	82.0	18.0	---	.980
	file length	-.43	.90	---				
(1)	(ridge spacing)	(1.0)	---	---	(100.0)	---	---	(.887)

TABLE VIII. RESULTS OF ONE-WAY MANOVAs ON RIGHT-SIDE MEASUREMENTS

Number of variables (p)	Parameters included in the best p-variable model	Correlations of variables with discriminant functions			Percent of inter- group variation accounted for by discrim. function			Eta- squared (1 - Δ)
		1st	2nd	3rd	1st	2nd	3rd	
5	elytral length	-.56	.34	-.07	67.4	29.5	3.1	.995
	no. of ridges	.78	.56	.15				
	file length	-.23	.81	.26				
	file width	.35	-.57	.66				
	ridge spacing	-.89	.41	.11				
4	no. of ridges	.75	.59	.23	67.1	30.6	2.3	.993
	file length	-.27	.79	.31				
	file width	.36	-.57	.73				
	ridge spacing	-.91	.37	.09				
3	no. of ridges	-.75	.61	.25	58.1	39.0	2.9	.990
	file width	-.37	-.56	.74				
	ridge spacing	.93	.35	.07				
2	no. of ridges	-.69	.72	---	69.2	30.8	---	.980
	ridge spacing	.96	.27	---				
(1)	(ridge spacing)	(1.00)	---	---	(100.0)	-----	---	.893

Δ is Wilk's lambda



$$\text{Discriminant function I} = .00012(\text{elytral length}) + .0076(\text{no. of file ridges}) \\ - .0038(\text{file length}) + .0059(\text{file width}) - .23(\text{ridge spacing})$$

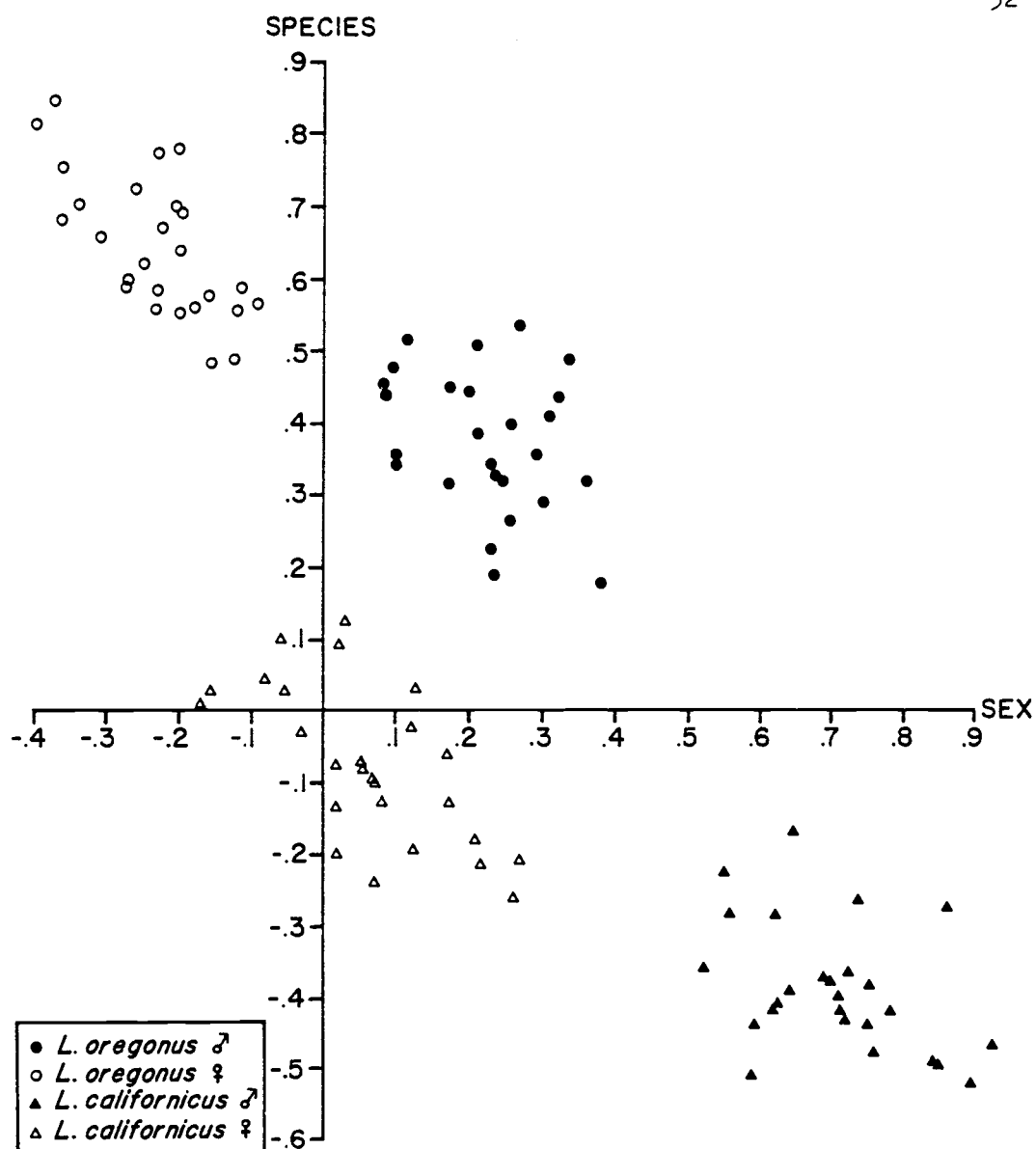
$$\text{Discriminant function II} = - .00022(\text{elytral length}) + .0099(\text{no. of file ridges}) \\ + .00046(\text{file length}) - .0054(\text{file width}) + .12(\text{ridge spacing})$$

(measurements in μ)

Fig. 10. Separation of male and female *L. oregonus* and *L. californicus* using first and second five-variable discriminant functions calculated in one-way MANOVA on left side data.

to a beetle. A similar complete separation in right side data is not illustrated. Plots of first and second discriminant functions in reduced models showed complete separation in the best four- and three-variable models, but with the species-sex groups clustered closer together. The best two-variable models did not achieve complete separation. Oddly enough, the "best" single variable, ridge spacing, was the first to be excluded from left side reduced models, undoubtedly because its information was also contained in file ridge number and file length. On the right side, the "worst" single variable, elytral length, was the first to be excluded from reduced models, as would be intuitively expected. All variables helped to separate the groups; tests for additional information (that the 5-p excluded variables would add to the p-variable model) were always significant ($P < .005$). Even in the best four-variable models, on both sides, the fifth variable would be able to further separate the four species-sex groups. The above manipulations simply demonstrate how different the species-sex groups really are. In a more extensive study, preliminary reduction of the number of parameters to be measured on subsequent larger samples could save research time. In this study, additional measurements were not time consuming, once each specimen was mounted on a slide. Elytral lengths, least effective in these Leperisinus species-sex groups, had to be measured so that beetle size could be considered when comparing their acoustic organs with those of other scolytids in subfamily Hylesininae.

Plots of species and sex discriminant functions, calculated in two-way MANOVAs, also separated the four species-sex groups completely using the full model (Fig. 11) and the best four- and three-variable models. Using the full model, there were species differences, sex differences but also interactions (all at $P < .0005$). Using a rule of thumb that the ratio of a main factor's Rao's F-approximation over the interaction's Rao's F-approximation should be at least 10.0, conclusive species and sex differences could be claimed for the right side (ratios 14.0 for species and 10.5 for sex) but not the left side (ratios 5.7 for species and 3.2 for sex). This was because sexual dimorphism was not always



$$\begin{aligned} \text{Species discriminant function} = & - .00021(\text{elytral length}) - .0046(\text{no. of file ridges}) \\ & + .0039(\text{file length}) - .0068(\text{file width}) + .26(\text{ridge spacing}) \end{aligned}$$

$$\begin{aligned} \text{Sex discriminant function} = & - .00018(\text{elytral length}) + .011(\text{no. of file ridges}) \\ & - .0021(\text{file length}) + .0025(\text{file width}) - .10(\text{ridge spacing}) \end{aligned}$$

(measurements in μ)

Fig. 11. Separation of male and female *L. oregonus* and *L. californicus* using species and sex five-variable discriminant functions calculated in two-way MANOVA on left side data.

the same in L. oregonus as in L. californicus. Correlations between variables and two-way MANOVA discriminant functions using the full models for left and right sides (Table IX) confirm univariate results. The following seven correlations, whose absolute values were over 0.7, correspond to the seven two-way ANOVA F-values over 200:

left file ridge number with sex
 left file length with species
 left file ridge spacing with species
 left file ridge spacing with sex
 right file ridge number with sex
 right file ridge spacing with species
 right file ridge spacing with sex

The correlation of right file length with the species discriminant function was not quite so high (.65) and neither was the univariate F-value (157.). This does not alter the basic finding that ridge number separates sexes, file length separates species, and ridge spacing does both.

TABLE IX. RESULTS OF TWO-WAY MANOVAs USING FULL MODELS

Side	Variable	Correlations of variables with discriminant functions			Percent of intergroup variation accounted for by discriminant function		
		Species	Sex	Inter-action	Species	Sex	Inter-action
left	elytral length	.63	-.55	.14	57.9	32.0	10.1
	no. of ridges	-.28	.78	-.54			
	file length	.71	-.25	.13			
	file width	-.52	.42	.42			
	ridge spacing	.91	-.93	.49			
right	elytral length	.65	-.44	.19	41.1	55.0	3.9
	no. of ridges	-.33	.91	-.70			
	file length	.65	.01	-.06			
	file width	-.60	.17	.41			
	ridge spacing	.97	-.73	.48			

Differences between left and right files

Table X indicates that the left file had more ridges, was shorter, and was much wider than the right file of the same beetle within each species-sex group. Only the width difference was obvious during measurement of specimens. The higher ridge density of left files is mainly due to the slanted orientation of right file ridges; no consistent differences

were obtained for ridge spacing. It is not known at what angle, or whether, right file ridges are struck during stridulation.

TABLE X. DIFFERENCES BETWEEN LEFT AND RIGHT SIDES
WITHIN LEPERISINUS SPECIES-SEX GROUPS

Structure and measurement	Mean difference (left minus right)			
	<u>L. oregonus</u>		<u>L. californicus</u>	
	Males	Females	Males	Females
Outside elytral length (μ) (crenulations to tip)	-7.2*	-4.4	0.0	-4.4
Inside elytral length (μ) (muscle attachment to tip)	-5.3	-1.7	13.3*	-8.6
Number of file ridges	5.8**	12.5**	11.6**	4.9**
Maximum file length (μ)	-25.2**	-34.2**	-45.9**	-43.0**
Maximum file width (μ) (perpendicular to median axis on right side)	53.1**	37.8**	44.2**	41.9**
Maximum file width (μ) (parallel to ridges on right side)	32.5**	14.2**	21.8**	15.8**
File ridge spacing (μ) (mean of 30 central ridges)	-.082**	-.064	.002	.134*
File ridge density per mm (ratio of no. to length)	28.8**	51.2**	94.7**	56.2**

*paired t-test shows significant difference at a .05 probability level

**paired t-test shows significant difference at a .01 probability level

Observation of the winglock mechanism, especially in color under the light microscope, suggested that the male's left scraper strikes approximately the middle of the left file, while his right scraper strikes the scaly gap on the left elytron between the file and the sutural margin (Fig. 12). This gap was wider than half the distance between scrapers in both L. oregonus males ($P < .001$, paired t-test) and L. californicus males ($P < .001$, paired t-test). The right scraper may strike the posterior end of the right file, where the gap narrows. Two assumptions, that the male stridulates with his elytra fully locked and moves his abdomen back and forth in a straight motion rather than twisting it, seem consistent with behavioral observations. The assumption that the scrapers are equidistant from the abdominal tergum's median axis is supported by their apparent symmetry with respect to the contour of the seventh abdominal tergite's posterior edge. The as-

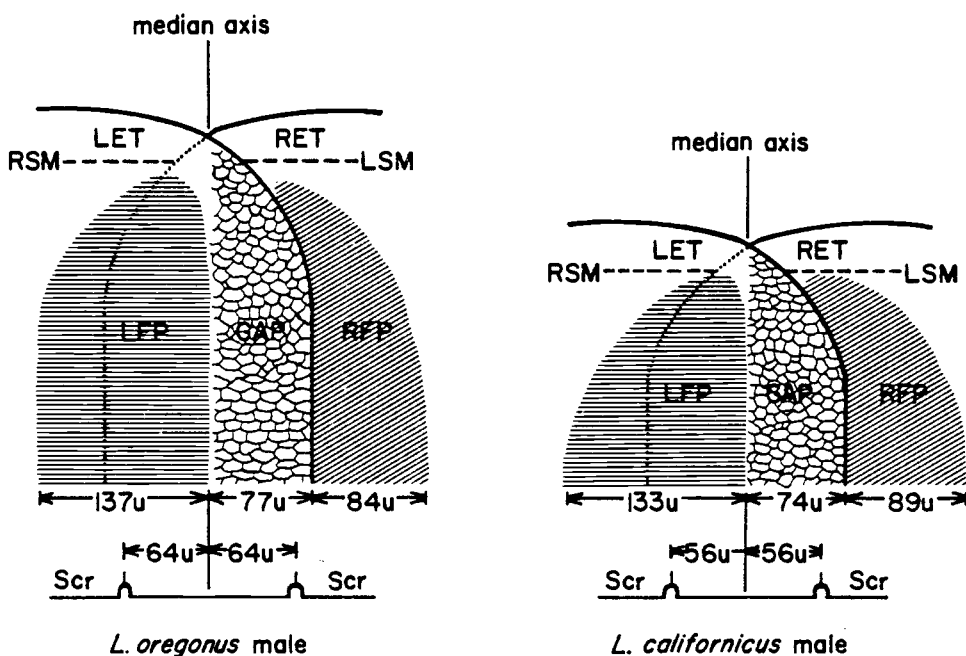


Fig. 12. Probable alignment of scrapers relative to files. Legend: GAP, scaly area between left file and left elytron's sutural margin, LET, left elytron's tip (inner surface); LFP, left file's posterior half; LSM, left elytron's sutural margin (heavy line); RET, right elytron's tip (inner surface); RFP, right file's posterior half; RSM, right elytron's sutural margin (dotted line)(behind left elytron in this diagram); Scr, scraper.

sumption that the left file's medial edge nearly coincides with the beetle's median axis is less supportable. It is based on a color change, from red on most of the elytron including the file to yellow on the scaly gap, which starts at the left elytron's tip. Only surgical removal of one file or the other, close observation of abdominal motion, and simultaneous listening could settle the question of which file(s) the male strikes.

Unusual specimens

Three of 52 male *Leperisinus* sampled had extra scrapers. One *L. californicus* had a third scraper 45 μ to one side of the pair 107 μ apart. One *L. californicus* had a third scraper 31 μ to one side of the pair 103 μ apart and a fourth scraper 33 μ to the other side. One *L. oregonus* had a third scraper 31 μ to one side of a pair 129 μ apart, as

well as two tube-like structures in the integument on either side of the scraper on the side with only one. These beetles were not judged to be seriously deformed, and the measurement mentioned for the "pair" was used. A tube-like structure reached the posterior margin of the seventh tergite, 15 μ to one side of a pair 95 μ apart, in one L. californicus male. Several L. oregonus males had one to at least four such structures which did not reach the margin of the seventh tergite.

Tube-like structures leading into the scrapers were illustrated in detail for Hylurgops rugipennis by Barr (1969), who distinguished cup-shaped and cone-shaped components. The reason for extra tube-like structures and scrapers in some Leperisinus males is unknown.

Variation within species-sex groups

Principal components analyses were done separately for left and right sides, making a total of eight analyses. The five variables chosen were the same as those used in MANOVAs (see above). Within each species-sex-side group, the five variables were always strongly inter-related ($P < .005$, Bartlett's sphericity tests). The first principal component accounted for 46.9 to 67.5 percent of the variation within a group and seemed to be a general "size" measure. It was always positively correlated ($P < .01$, except for one r significant at $P < .05$) with elytral length, number of ridges, file length and file width. The first two principal components together accounted for 75.3 to 86.5 percent of the variation within a group. The second principal component seemed to be a "spacing" measure. It was always correlated ($P < .01$) with ridge spacing, positively in six species-sex-side groups and negatively in two. The third and fourth principal components were always less than 1.0 so were not important in accounting for within-group variation.

In each species-sex-side group, two to four of the four file variables were correlated with elytral length. One to four of the six possible intercorrelations among file variables were significant. It was natural to ask whether these variables would still be intercorrelated after the influence of elytral length was removed by multiple partial correlation.

After this was done, one to three of the six remaining correlations were significant. However, the only partial correlation that was significant in each of eight species-sex-side groups was number of ridges with file length ($r=.50$ to $.81$, $P<.01$). This would be expected, since ridge density is quite uniform within each group.

To examine correlations between left and right files within each species-sex group, four canonical correlation analyses were done using only the file variables: number of ridges, file length, file width, and ridge spacing. In each group, left and right files were related ($P<.005$, Bartlett's tests). The first canonical correlations were $.81$ to $.89$, and one to three pairs of canonical variates were useful. The redundancy of right file data given the availability of left file data was 33.2 to 49.9 percent. The redundancy of left file data given the availability of right file data was 37.7 to 58.7 percent. This simply demonstrates that Leperisinus spp. left and right files were intermediate between being totally unrelated and completely correlated.

Comparisons with other scolytids

L. oregonus and L. californicus males are intermediate in size between the larger Dendroctonus brevicornis and the smaller D. frontalis, using inside elytral lengths in Michael and Rudinsky (1972). File length of L. oregonus is close to that of D. brevicornis, whereas that of L. californicus is closer to that of D. frontalis. Number of ridges (or teeth) per file in these Leperisinus spp. is 1.5 to 2.5 times the number in those two Dendroctonus spp. Among four larger Dendroctonus spp., D. pseudotsugae has the most ridges (or teeth), but its maximum is near the Leperisinus spp. average. The most striking difference is that the Leperisinus spp. have much denser ridges than any of the Dendroctonus spp., with only D. frontalis approaching L. oregonus but still about 50 ridges per mm less. Another difference is that the two Leperisinus spp. scrapers are about 2.5 times as far apart as in D. brevicornis and 4-5 times as far apart as in D. frontalis. They are also further apart than in the larger Dendroctonus spp. This supports Barr's (1969) prediction of an array of distances between processes in

the Hylesininae. Lekander (1969) listed Leperisinus and Hylesinus among "derivative Hylesinides sensu Nüsslin" and Dendroctonus among "archaic Hylesinides" based on larval morphology. Possibly, distance between processes is another character manifesting division within subfamily Hylesininae, but data from related genera are scarce. Distance between processes, and their alignment with respect to the files, may influence how the beetle moves to produce sound.

Rudinsky and Vallo (in press) measured L. fraxini male left elytra and files. Their elytra are similar in length to those of L. oregonus and L. californicus, or slightly longer. File length is intermediate between our Oregon species, ridge number is slightly less and ridge spacing is similar to L. oregonus and does not overlap with L. californicus. It would be interesting to know the file dimensions of L. orni, a European species sympatric with L. fraxini.

Leperisinus spp. do not make a record for number of ridges and ridge density of the pars stridens of scolytids. Ips pini (Swaby and Rudinsky, 1976) had seven to eight times the number of ridges and about ten times the number of ridges per mm as L. oregonus and L. californicus. However, this species has a vertex-pronotal type of stridulatory apparatus and is in a different subfamily. Comparisons are probably best confined to within groups of species with qualitatively similar acoustic organs.

Behavior

L. oregonus pairing

When a male was placed near an attractive female gallery entrance, he sometimes hesitated briefly before digging through and pushing away any frass which blocked it. He then descended, head first, into the gallery until apparently contacting the female. Some males which disappeared rapidly below the bark surface were later pushed backwards by the female. Most males had to overcome female resistance by shoving, and a few scratched her elytra quickly and/or rhythmically. Only three females seemed unusually aggressive; they pushed the males out of the

gallery onto the bark surface and sometimes further backwards but eventually allowed their energetically stridulating partners to reenter.

Of 24 males observed, 22 stridulated. Those which were timed began producing intermittent series of chirps (Plate V, A-F) at 0-6 min after locating the entrance ($\bar{x}=1.31$, $SE=0.37$, $n=16$). These series were most frequent (24 per min, $n=1$) during attempts to enter, less frequent (15 per min, $n=1$) once the male's declivity was flush with the bark surface, and infrequent (0-7 per min) once he was well inside. A few males chirped less frequently just after locating the female but stridulated almost continually when tactile interactions became aggressive. Sharp clucking sounds were produced in one of the most active situations, in addition to series. One of the two silent males backed out and left a female gallery about four min after entering halfway. The other silent male remained halfway in the entrance, just making soft scratching noises associated with position changes, for 15 min, after which rival males were introduced, one of which dislodged him. All but one stridulating male, also presented with a rival, gained entry to a female gallery.

Most males descended below the bark surface by 0-17 min ($\bar{x}=7.46$, $SE=1.41$, $n=14$), but one occasional chirper took 42 min to enter. One raspy-sounding chirper, which produced only about four series, took 137 min to enter. The others were not timed. Once established, the male removed frass from the gallery. No mating was observed at the gallery entrance, but larvae were produced in all but one of the galleries.

L. californicus pairing

Of 52 pairs, 25 mated at the gallery entrance, and accurate timing was obtained for 23. Seven males attempted to position themselves for mating but appeared unsuccessful. Eighteen males made no attempt to mate. Two males were (accidentally) interrupted during mating or positioning. The first three groups will be discussed below. Interesting behavioral elements noted in laboratory-fed non-audiorecorded pairs will be mentioned afterwards.

(i) Pairs which mated

Duration of premating behavior, from the time the male located the gallery entrance, was 1-46 min ($\bar{x}=16.41$, $SE=2.76$, $CV=80.7$ percent, $n=23$). The shortest duration occurred at a shallow gallery with little frass. The longest duration occurred at a gallery from which the male removed considerable amounts of frass before even stridulating. Males dug through any frass blocking the entrance. Seventeen of 25 entered immediately, head first, but most of these later backed out. Five encountered the female at the surface, one encountered her partway in, and initial behavior of two was not noted.

All but one of 25 males produced intermittent series of chirps (Plate VI, A-E). Most began from 0-13 min after locating the gallery entrance ($\bar{x}=4.43$, $SE=0.80$, $n=23$), but one made a single chirp at six min and waited until 33 min to produce series of chirps. The "silent" male was observed only visually, so he might have stridulated inside the gallery during the initial three min before backing out to remove frass. Soft, small chirps as well as series were produced by one male. Stridulation seemed most intense prior to mating.

Males on the bark surface faced the entrance but frequently moved clockwise or counterclockwise between periods of stridulation. Some turned away, as if to leave, but then turned back and resumed premating behavior. Males partly in the entrance merely rotated. They backed up to the entrance, sometimes to remove frass but sometimes struggling and apparently pushed by the female. The male pushed the female's declivity with his frons and, less often, touched it with his antennae or mandibles. Some also pushed at her sternum. Several males scratched her elytra quickly and/or rhythmically or slowly scraped her elytra with their mandibles either during or especially between series of chirps.

Females were rarely seen to do more than block the entrance with their declivities or to protrude their abdomens above the bark surface so that the posterior abdominal sternites were exposed. The latter position may have signalled readiness for mating. Some surfaced and descended again. Only one aggressively pushed a male away; he returned and made stridulatory motions typical of single chirps between series.

In seven pairs, the male climbed onto and off of the female from one to six times ($\bar{x}=2.1$) before actually mating. These attempts were distinguishable from copulation by the male's unsteady movements and, within a minute, return to a position facing the female. Three males cleared frass from her abdomen between some attempts. The reason for this behavior is unknown. It may be attributable to the rougher edge and greater diameter of a drilled hole as opposed to a natural one. It may, however, be a facultative part of L. californicus premating behavior. It was not observed in any L. oregonus.

Just before copulation, the male ceased stridulation, climbed onto the female and became relatively calm. No stridulation occurred during mating, but the silence was sometimes broken by soft, scratching noises. Antennae were pointed downwards in the 12 males for which antennal position was noted. The male's body was usually at a $30-45^{\circ}$ angle to the bark surface. It ranged from nearly parallel, when the female protruded from the entrance, to nearly perpendicular, when she was further in the gallery and he was inside the entrance. The male braced his body with his prothoracic legs on the bark and with his mesothoracic legs on the bark or on the female. Twelve of 23 males stroked the female's posterior sternites with one or both metathoracic legs at a rate of 75-150 times per min ($\bar{x}=108.5$, $n=4$). Eleven of 23 males pushed their abdominal tip repeatedly against that of the female. This was accompanied by a rocking motion of the body and head, occurring at a rate of 60-120 times per min ($\bar{x}=90.4$, $n=5$). It is probable that stroking and pushing motions are synchronized.

One male was observed closely enough to ascertain that, while his abdominal tip bent up and down, the translucent aedeagus moved slowly out of and into the female. This occurred at least six times during the 8 min 10 sec mating.

Mating duration was 3.75-9.5 min ($\bar{x}=6.94$, $SE=0.28$, $CV=19.3$ percent, $n=23$). Disengagement was usually sudden and rapid. One male mated with a second female 36 min after disengaging from the first partner.

Postmating behavior varied considerably among the 23 pairs (which were timed during mating). Only two males left immediately and without stridulating, whereas 21 attempted to push their way into the gallery.

Their behavior had elements of premating behavior but appeared quite aggressive. The male faced the female and often scratched her elytra quickly and rhythmically. He used his mandibles to either make rapid back and forth motions across her elytra, repeated backward scraping strokes, or repeated forward head thrusts which also hit the elytra. He sometimes climbed on the female during these activities. Most males butted the female declivity from behind with their frons, and one touched it with his antennae and mandibles as well. One held the female's posterior abdomen with his legs. Several turned away from and back towards the female or even left and returned.

Sixteen of 23 males stridulated from 0-8.5 min after disengagement from copulation ($\bar{x}=2.11$, $SE=.77$). As in premating, most chirps were in intermittent series. One male also made some small, ungrouped chirps after pushing and scratching the female. Stridulation seemed unrelated to male success in entering the gallery after mating. Of the 13 males admitted, six chirped immediately, three in 0.5-8.5 min and four not at all. Of the eight males not admitted, one chirped immediately, six in 0.5-8.5 min and one not at all.

Postmating rejection of males seemed linked to female excavation and oviposition. These L. californicus had been trapped to cages containing infested logs and were not necessarily virgins. Seven of the eight rejecting females, whose galleries were excised the day of observation, had 7-18 eggs per gallery and had been introduced to the log at least one week previously. The eighth female had larvae in her gallery system by 24 days after the behavioral observations, so her brood could have been only of the male observed to mate with her in the laboratory. Of the 13 females which admitted males to their galleries, two had only 1-4 eggs per gallery despite having been introduced one week previously. Five others had no eggs, short galleries, and had been introduced only 1.5-2 days previously. Some galleries were not examined.

The surprise is not that ovipositing females prevented males from entering their galleries, but that males seemed so determined to enter. Seven of the eight rejected males remained at the gallery entrance between 22.5-151.5 min after disengagement from copulation ($\bar{x}=66.88$,

SE=21.01), and the eighth was still at the entrance at 127 min. Males admitted to galleries were not in until .75-72.67 min (\bar{x} =19.67, SE=6.10, n=12), and one was only partly in at 107.5 min, because the female had not excavated far enough for him to fit.

Females guarded their gallery entrances by keeping their declivities flush with the bark.

(ii) Pairs in which the male attempted to mate

These seven males, observed without acoustic equipment, all made stridulatory motions. Most began at 1-6 min (\bar{x} =2.50, SE=0.76, n=6), but one waited until 24 min. Males made one to seven mating attempts each (\bar{x} =2.9). Most were brief and only involved climbing onto and off of the female (n=14), stroking the female with his metathoracic legs as she moved toward the bark surface (n=1), or stroking accompanied by unsteady movements and small stridulatory motions (n=1). Three other 1-2 min "attempts" could have been brief copulations, but the male made a renewed attempt only 1.5 min after one of these. In the longest "attempt" (3.5 min) the male's abdomen appeared unjoined to that of the female. Some females seemed uncooperative. They pushed the male backwards many times and even abruptly out of the entrance. Of the seven males, four were admitted between 14 min after locating the female and the next day, two left between 8-13 min, and one was removed after 68 min. An eighth male, accidentally disturbed during his second positioning attempt, was audiorecorded making sharp clucking chirps (Plate XIII, A-C) inbetween his series and during his first positioning attempt.

(iii) Pairs in which the male did not attempt to mate

Premating behavior in these 18 pairs was straightforward and included most elements observed in L. californicus which did mate. Only the 14 pairs observed in 1976 will be discussed, since 1975 notes were less detailed. Ten of these 14 males stridulated, intermittently in series (as did the 1975 males), one very softly. Most began 0-7 min after

locating the female gallery entrance ($\bar{x}=3.72$, $SE=0.75$, $n=9$), but one waited until 23 min and produced only one series. Of the four "silent" males, three were observed without acoustic equipment, and one emitted a single squeak at 22 min.

Eight of the ten stridulators were admitted to galleries. Most entered by 0-28 min after locating the female ($\bar{x}=12.71$, $SE=3.68$, $n=7$), but one did not enter until 47 min. Two males left at 1-3 min. The four "silent" males were all admitted, between 0-30 min.

Of the four males which entered immediately, one backed out covered with frass but gained readmission. The other ten males spent varying time periods at entrances before either getting in or leaving.

(iv) Laboratory-fed non-audiorecorded pairs

Premating behavior was similar to that observed in field-collected L. californicus. Males would not leave the female's gallery entrance voluntarily. When artificially blocked by a piece of minuten (minute nadelin) fastened across the entrance, at least eight males pulled at the obstacle with their mandibles, and three also bit off bark around the entrance. Nine males attempted to mate at female gallery entrances, even if blocked by a minuten and even if the female had eggs in her gallery. Some were observed making stridulatory motions. Some moved their antennae quickly on the female's elytra.

Antennal movements by two males were noted during copulation at female gallery entrances. One made jerking motions of the antennae, which moved towards the ventral midline at irregular intervals, accompanied by jerking motions of the body and metathoracic legs. The other held his antennae outwards and downwards, moving them outwards and then slowly inwards at intervals of several seconds while making slight head motions. Undoubtedly, field-collected beetles also made antennal movements during copulation which were not noted due to preoccupation with other behavioral elements and with audiorecording.

L. oregonus rivalry

Rivalry behavior was difficult to elicit. No distinctive signal, such as the interrupted chirp of Dendroctonus pseudotsugae, was found.

Males (rivals) were placed near attractive female galleries into which another male (resident) had already entered part way. Those rivals exhibiting moderate response antennated the resident, pushed him or climbed on him, but few chirps were produced. A few rivals were persistent enough to leave and return several times. The resident either remained wedged in the entrance, continued his pre-mating behavior, or shoved the rival backwards.

Two rivals succeeded in dislodging resident males. They employed different methods, both gradual. In the first case, the rival chewed a second entrance in the bark, which intersected with that of the female, and forced the resident towards the surface. By two hours, the resident had only his head in the entrance. At 3 hours 48 min, the rival descended under bark while making slow abdominal motions. The displaced resident remained at the entrance for over an hour, after which observation was discontinued. Stridulation, monitored during the first 1.5 hours, consisted mainly of intermittent series of chirps, typical of premating, produced by both males. Only a few single, ungrouped chirps were noted. In the second case, the rival dislodged the resident from the original, female entrance. He antennated him, bit him, scratched his declivity, wedged in next to him, pried him forward by pushing against his sternum, and climbed onto him. Soft, single, ungrouped chirps (Plate VII, D-F) were audiorecorded soon after the rival had been pushing the resident from behind or from the side. A few more were heard while he pressed the resident's sternum to force him forward. At 1 hour 27 min after the rival located the gallery, he pushed the resident out and away, into the frass. The resident left and returned seven times in the next 21 min, at first behaving aggressively, being pushed and landing on his back. A few chirps were produced during later approaches, while he was climbing on the rival. Chirps in these two "natural rivalry" situations appeared to be produced by the resident, possibly in protest against the rival's dislodgement

activities.

Other efforts to elicit rivalry stridulation included use of a walkway leading to a male boring in a drilled hole, confinement of males by twos in drilled holes or in artificially cut bark crevices with or without female frass, and shoving males into galleries already containing an established male-female pair. Only two situations (males head-to-declivity in a drilled hole and males head-to-head in an enlarged crevice) yielded enough chirps for audiorecording. These may have been stress sounds protesting confinement rather than territorial signals.

Since the few "natural rivalry" situations, at female galleries, did not involve very aggressive behavior, further observations would be necessary before ruling out the existence of a true rivalry signal in L. oregonus.

L. californicus rivalry

Rivalry behavior was difficult to elicit but was quite aggressive in some instances. No distinct rivalry signal, such as the interrupted chirp of Dendroctonus pseudotsugae, was recorded.

The one "natural rivalry" recording had chirps (Plate VIII, D-E) similar to stress, made while the rival was dislodging the resident. The rival located the attractive female gallery shortly after the resident. Within two min, both males were chirping intermittently in series. The single, ungrouped rivalry chirps occurred at 7 min and dislodgement occurred at 15 min. It was thought, but not ascertained, that the resident made the rivalry chirps.

Six brief but active conflicts occurred at attractive female galleries and involved field-collected L. californicus. They lasted 1-5 min. Behavior was not uniform. Aggressive back and forth pushing in head-to-head clashes on the bark surface occurred when a rival drove away a resident. In five cases, the resident remained. He chased the rival on the bark surface from the rear, shoved him briefly with his head or declivity, climbed backwards onto his head and made stridulatory

motions, or remained wedged in the gallery entrance while being pushed.

Only two lengthy, active conflicts occurred at attractive female galleries. They involved laboratory-fed L. californicus. They lasted 40 min and 13 min and encompassed ten and five clashes, respectively. Each clash lasted 0.5-5.0 min and consisted mainly of aggressive back and forth pushing while head-to-head on the bark surface within four cm of the gallery entrance. The males' antennae waved rapidly. Slow abdominal motions were occasionally noted. Once, a resident caught a rival's left femur in his mandibles and held it while pushing him. Inbetween clashes, both males returned to the female and made stridulatory motions typical of premating series. Sometimes, both returned simultaneously. Usually, either the rival returned before the resident or vice versa. In both cases, the resident lost the conflict and either wandered over the log or fed in an abandoned gallery. Such prolonged conflicts may rarely occur in the field. A male which momentarily loses his grip while on the underside of the log would fall off, and a male which remains on the log might find another female gallery nearby instead of returning to the first one.

Since the most convincing, aggressive "natural rivalry" situations were observed in the absence of acoustic equipment, further work should be done before ruling out the existence of a true rivalry signal in L. californicus.

Field observations

Field notes on Leperisinus spp. behavior do not contradict laboratory observations.

L. oregonus males wandered over the log surface with their antennae spread. They sometimes entered and left several gallery entrances. Some were covered with partly crystallized sap. Males were seen partly inside gallery entrances, making intermittent series of stridulatory motions and removing frass. If the light colored male was removed, a dark colored female was found inside. Males frequently took as long as three to seven hours to move from the bark surface to well inside the

entrance, often because the female had not excavated far. Pairing activity was observed as early as 11:10 A.M. and as late as 8:25 P.M., but seemed highest in mid-afternoon.

L. californicus were also observed wandering over the bark, mainly in late afternoon but up to sunset. Intermittent series of stridulatory motions identified some as males, and others were labeled by their behavior and/or location relative to the entrance and sexed in the laboratory. Some males made jerky motions characteristic of males scratching the female elytra. One was found in mating position at a gallery entrance, remained so for four min, disengaged, went head first part way into the gallery and made stridulatory motions. The female of another copulating pair had bored only a head's length into the bark. Brief rivalry behavior was observed. One L. californicus was antennating and pushing a male from behind. The latter was already part way in the female gallery, and the intruder soon walked away. Another intruder walked away from an entrance after being pushed. A third intruder made intermittent stridulatory motions but fell to the grass when pushed by the outer, male occupant whose female was further inside.

These observations suggest that L. californicus has a greater variety of behavior than L. oregonus in natural ash stands as well as in the laboratory. Further study would require bark sandwich introductions (as in Reid, 1958 and others) so that in-gallery behavior could be observed.

Comparisons with other scolytids

Observation of courtship and mating on the bark surface and/or at gallery entrances is not unprecedented among scolytids. Chapman (1910) noted that Scolytus multistriatus copulation at gallery entrances lasted 5-10 min. Bartels and Lanier (1974) found S. multistriatus "constantly engaging in courtship behavior at the gallery entrance" but few males in excised galleries, indicating that their visits were short. Their laboratory work on this species (ibid) confirmed its ability to mate on elm twigs and on shredded paper toweling as well as the ability of one male to fertilize several females. Goeden and Norris (1964) observed

repeated copulations of S. quadrispinosus during initial egg-gallery construction in the field and judged this species to be facultatively polygamous and polyandrous. Petty (1977) observed Trypophloeus populi mating with females just initiating galleries, at gallery entrances of those already bored in and inside galleries. Another aspen bark beetle, Procryphalus mucronatus, sometimes mated before gallery initiation; its copulation was commonly repeated and took 3-10 min after a 3-30 min premating period (ibid). These time periods are similar to those which I observed in L. californicus. Both T. populi and P. mucronatus had species-specific tactile premating rituals, involving repeated mounting attempts and stroking in both species as well as the male brushing the female's posterior abdomen with his mandibles in the latter (ibid), which seem more stereotyped than tactile aspects of Leperisinus spp. behavior.

Duration of L. californicus mating appears similar to that of Dendroctonus pseudotsugae (4-6 min, Rudinsky and Ryker, 1976) and D. ponderosae (3.5-5 min, Ryker and Rudinsky, 1976b) but longer than that of D. frontalis (133 sec, Yu and Tsao, 1967) and D. monticolae (= D. ponderosae, 30 sec, Reid, 1958). Unlike L. californicus, Dendroctonus spp. generally mate inside the gallery.

Pairing behavior has not been described in detail within Leperisinus Reitter. Simmel (1924) noted that L. orni were in copula during boring. Del Guercio (1931) stated that L. fraxini mated on olive branches before gallery initiation and that copulation took a long time. Chararas (1958) stated that L. fraxini females bore part way into the bark, await a male's arrival and mate soon afterward. Generalizations on behavior of this genus would be premature, since so few species have been observed.

Stridulation

Qualitative description

Sounds produced by L. oregonus and L. californicus males were qualitatively similar and occurred in one of two patterns, depending on the

Oscillograms of L. oregonus and L. californicus male stridulation - I

- Plate IV Summary of chirps at the same time scale. L. oregonus (A) single stress chirp, (B) double stress chirp (uncommon), (C) single natural rivalry chirp, (D) double natural rivalry chirp (uncommon), (E) premating "skipper" chirp (uncommon) from series in which one of the two directions of motion is not acoustically effective, (F) premating major chirp followed by minor chirp, (G) premating major chirp followed by minor chirp, in a different male; L. californicus (H) single natural rivalry chirp; (I) stress chirp followed by extra minor-type chirp (uncommon, and this male with larger than average stress chirps), (J) premating major chirp followed by premating minor chirp, (K) premating "crunchy" chirp (uncommon). Legend: cr, crunchy chirp; maj, major chirp or component; min, minor chirp or component; sgl, single chirp; skp, skipper chirp.
- Plate V L. oregonus premating stridulation. (A) two series with scratching inbetween, (B) first series, (C) major chirp, sixth in series 1, (D) minor chirp, seventh in series 1, (E) toothstrikes in major chirp, (F) toothstrikes in minor chirp.
- Plate VI L. californicus premating stridulation. (A) one series, (B) major chirp, third in series, (C) minor chirp, fourth in series, (D) toothstrikes in major chirp, (E) toothstrikes in minor chirp.
- Plate VII L. oregonus stress and rivalry stridulation. Stress (A) many successive stress chirps, (B) one stress chirp, fourth in Fig. A, (C) toothstrikes in stress chirp; rivalry (D) many successive natural rivalry chirps, (E) one natural rivalry chirp, fifth in Fig. D, (F) toothstrikes in natural rivalry chirp.
- Plate VIII L. californicus stress and rivalry stridulation. Stress (A) many successive stress chirps, (B) one stress chirp, eighth in Fig. A, (C) toothstrikes in stress chirp; rivalry (D) many successive natural rivalry chirps, some obscured by scratching noises, (E) one natural rivalry chirp, seventh in Fig. D, (F) toothstrikes in natural rivalry chirp.

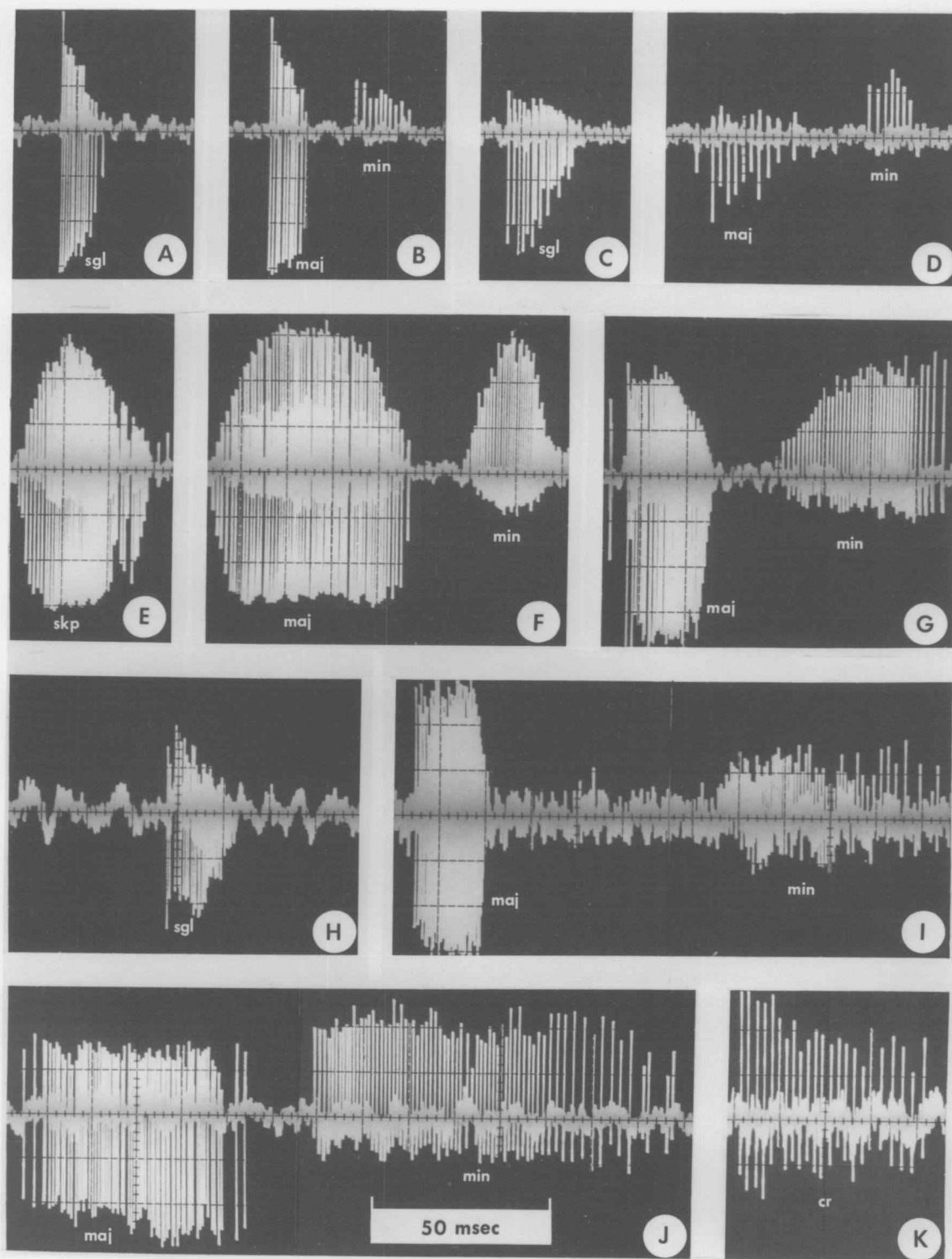


Plate IV

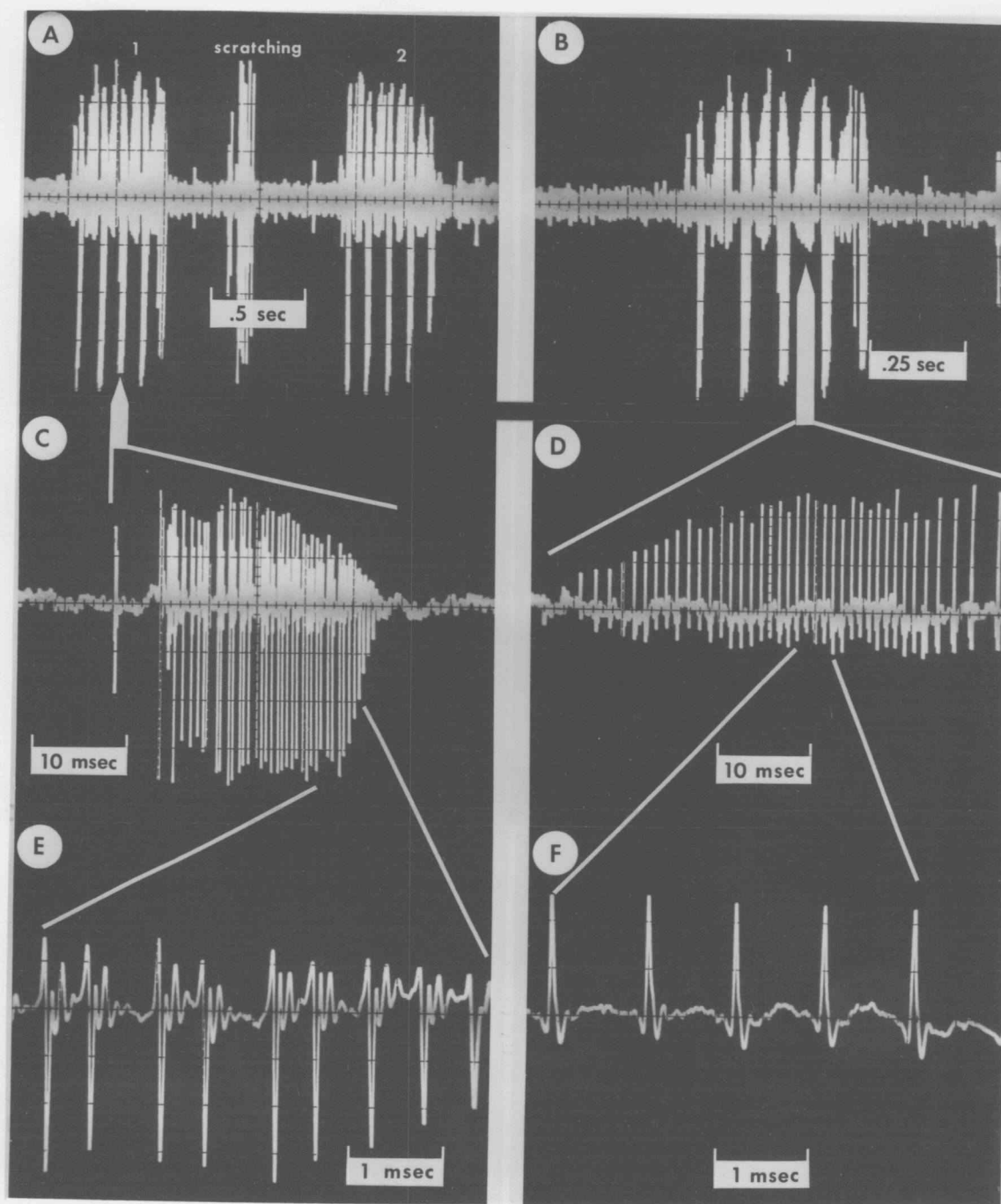


Plate V

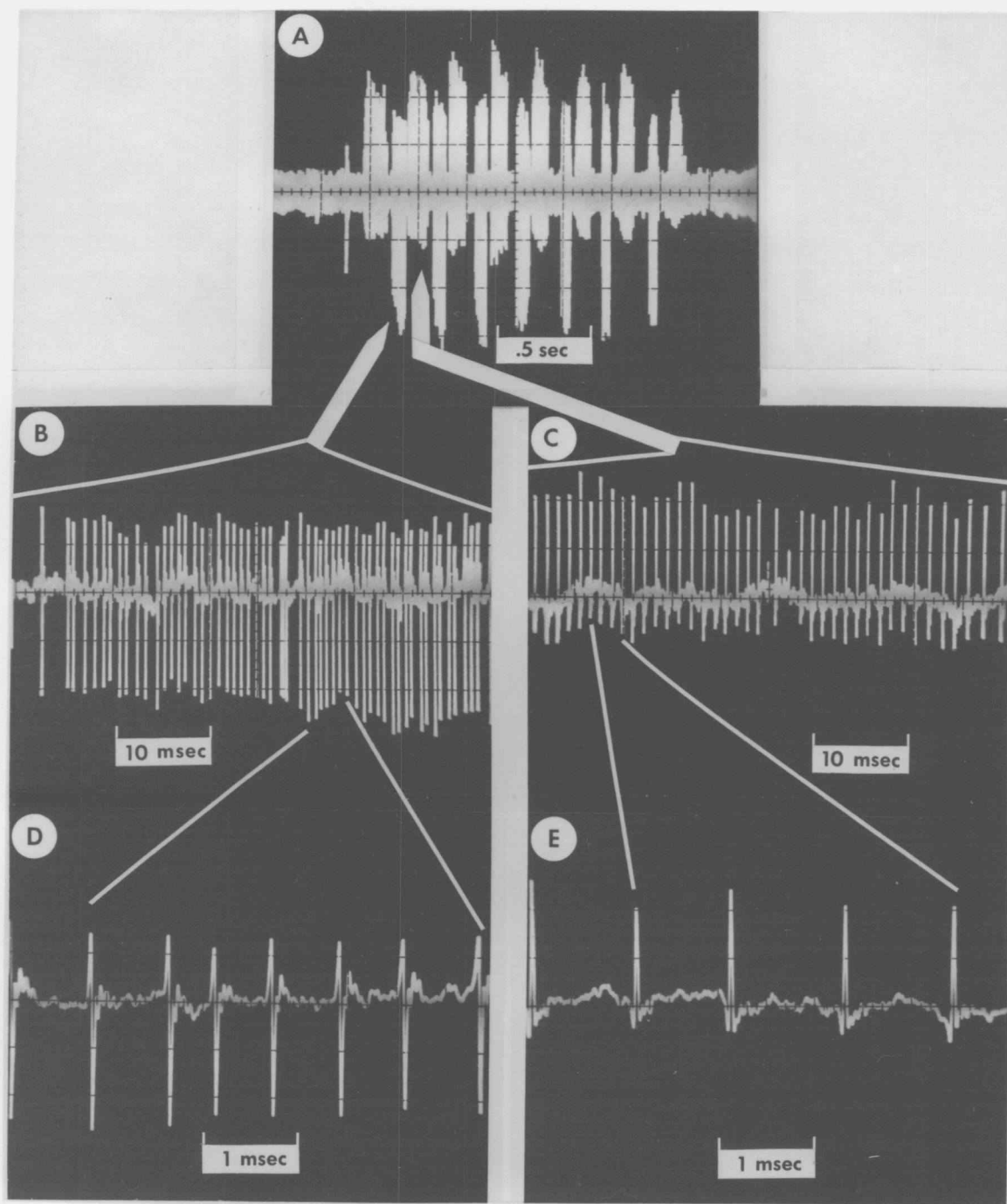


Plate VI

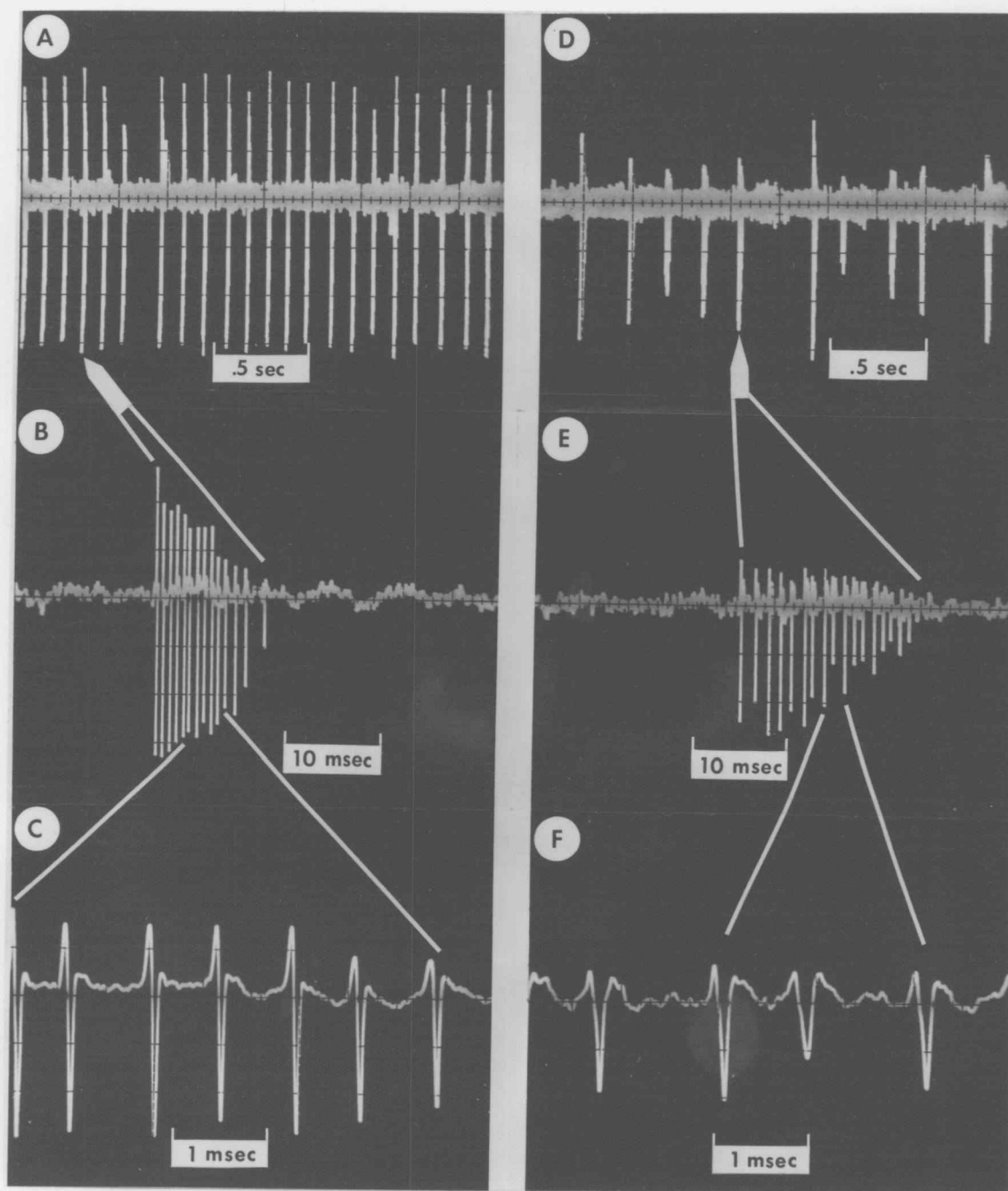


Plate VII

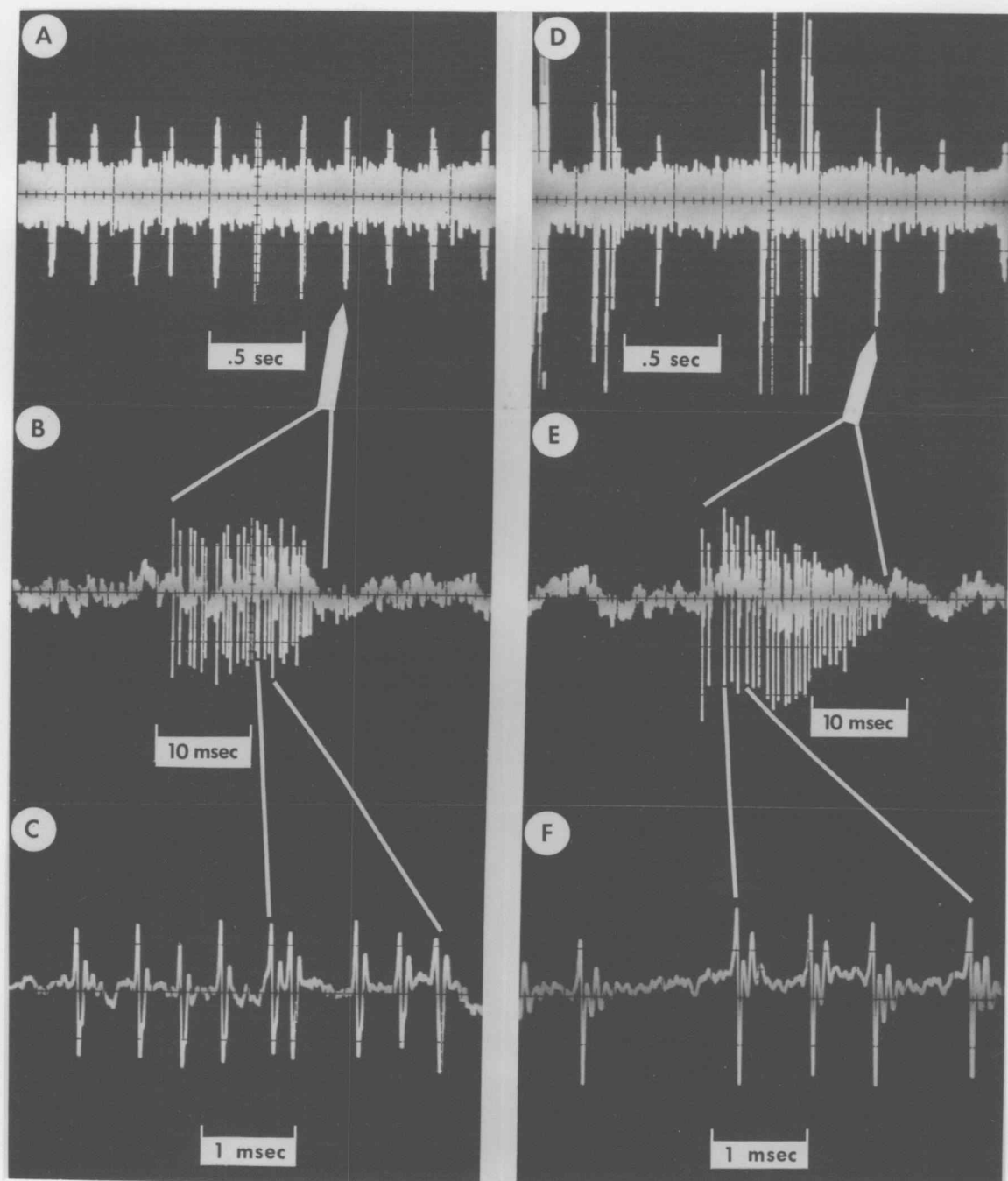


Plate VIII

behavioral situation. No detectable or distinguishable sounds were elicited from females of either species.

Oscillograms illustrate typical stridulation of L. oregonus males (Plate IV A, C, F, G; Plate V A-F; Plate VII A-F) and L. californicus males (Plate IV H, J; Plate VI A-E; Plate VIII A-F). Descriptive statistics for typical chirps, series of chirps and chirp rates are presented in Tables XI, XII and XIII. Broughton (1963) defined "chirp" as "the shortest unitary rhythm-element of a sound emission that can readily be distinguished by the unaided human ear." A "series" is simply a group of chirps separated from other groups of chirps by a gap of at least .375 to .5 sec, usually longer.

In premating and postmating situations, a male was at or just inside of a female's breeding gallery entrance. He produced intermittent series of 3-42, usually 5-15, chirps. These series were separated by silences, scratching noises or, rarely, ungrouped chirps. Chirps in series were of two alternating types designated "major" and "minor." Major chirps usually had greater total amplitudes than minor chirps and sounded louder, so my unaided ear heard a series as accents alternating with soft sounds. Although I had difficulty distinguishing these sounds if delivered at rates over about 15 per sec, they were always distinct at half speed, occurred in the same pattern as those produced by males which stridulated more slowly, and were represented on the oscilloscope by separate "envelopes" (groupings) of "toothstrikes" (sound pressure impulses). Therefore, I feel justified in calling them "chirps" without strictly adhering to Broughton's requirement that the ear be unaided. Major chirp toothstrikes were mostly below the baseline, and each toothstrike's largest excursion away from and back to the baseline was down and then up, on our apparatus (Plate V E, Plate VI D). Minor chirp toothstrikes were mostly above the baseline, and each toothstrike's largest excursion away from and back to the baseline was up and then down, on our apparatus (Plate V F; Plate VI E). Compression and rarefaction are related to upward and downward excursions of the oscilloscope signal, but it has not been determined which is which (R. R. Michael, verbal communication). Each pair of major and minor chirps (Plate IV F, G, J) appeared to be produced by one cycle of back and forth motion of

TABLE XI. STRESS, RIVALRY, PREMATING AND POSTMATING CHIRPS
OF LEPERISINUS OREGONUS AND L. CALIFORNICUS

SP- YR	SITU	TYP	n	n	No. of toothstrikes				Duration (msec)				No. of toothstrikes per sec			
					Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
OR	STR	SGL	5	75	12.6	6- 27	0.58	40.2	9.6	3.0- 22.3	0.51	45.7	1386.	764.-3000.	45.2	28.2
OR	RIV	SGL	3	45	14.2	5- 22	0.62	29.4	13.5	3.8- 22.3	0.71	35.3	1098.	557.-1702.	32.2	19.7
CFL	STR	SGL	6	90	23.9	4- 67	1.74	69.2	13.7	2.5- 44.0	0.83	57.2	1715.	640.-3304.	65.4	36.1
CL	RIV	SGL	1	15	29.5	8- 58	3.64	47.7	17.2	6.8- 26.0	1.35	30.3	1676.	962.-2600.	145.7	33.7
OR	PRE	MAJ	6	90	57.5	14- 93	2.01	33.1	36.9	8.3- 38.5	1.33	34.1	1651.	556.-3520.	61.4	35.3
		MIN		90	56.5	22- 87	1.66	27.9	41.6	18.0- 66.5	1.19	27.1	1369.	992.-1459.	21.4	14.8
RG	PRE	MAJ	10	150	37.5	6- 70	1.08	35.4	24.8	5.8- 23.3	0.63	31.2	1584.	581.-4870.	47.1	36.4
		MIN		150	39.2	10- 68	1.07	33.5	39.2	11.5- 45.5	0.79	24.7	998.	393.-1049.	19.4	23.8
CF	PRE	MAJ	6	90	77.5	23-118	2.35	28.8	40.5	18.0- 58.0	1.10	25.8	1914.	1278.-2917.	33.1	16.4
		MIN		90	73.9	13-125	2.50	32.0	60.4	11.0- 96.0	2.21	34.8	1309.	400.-2149.	41.5	30.1
CL	PRE	MAJ	9	135	78.0	32-122	1.69	25.2	48.7	19.8- 90.5	1.17	27.8	1679.	927.-2675.	39.6	27.4
		MIN		135	74.7	36-119	1.74	27.0	77.0	40.5-122.5	1.43	21.6	991.	404.-1584.	20.7	24.3
CFL	PRE*	MAJ	5	75	75.4	23-119	2.19	25.1	46.1	18.0- 90.5	1.97	37.0	1762.	952.-2607.	52.6	25.8
	PRE*	MIN		75	74.6	34-125	2.38	27.6	73.4	26.0-109.5	2.15	25.4	1034.	558.-1615.	21.6	18.1
	POST	MAJ		75	74.5	26-108	1.96	22.7	46.6	19.3- 81.0	2.07	38.5	1739.	981.-2602.	51.8	25.8
	POST	MIN		75	71.7	30-114	2.13	25.7	67.1	40.5- 98.5	1.47	18.9	1072.	589.-1562.	24.5	25.8

Abbreviations: CF, 1975 L. californicus; CFL, 1975-76 L. californicus; CL, 1976 L. californicus; C.V., coefficient of variation (percent); MAJ, major; MIN, minor; n ~~33~~, number of males in group; n OBS, number of observations (chirps) in group; OR, 1975 L. oregonus; POST, postmating; PRE, premating; PRE*, premating by males which also chirped after mating; RG, 1976 L. oregonus; RIV, rivalry; S.E., standard error of the mean; SGL, single; SITU, situation; SP-YR, species-year group; STR, stress; TYP, chirp type

TABLE XII. PREMATING AND POSTMATING SERIES OF LEPERISINUS OREGONUS AND L. CALIFORNICUS

SP- YR	SITU	n	n	Number of chirps				Duration (msec)				No. of chirps per sec			
				Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
OR	PRE	6	60	10.4	4-21	.352	26.2	631.	215.0-1410.	22.9	28.1	16.7	11.5-19.8	.266	12.4
RG	PRE	10	98	10.1	3-15	.203	20.0	523.	145.0- 835.	11.6	21.9	19.4	15.2-22.0	.165	8.4
CF	PRE	5	49	12.8	4-32	.906	49.6	1242.	350.0-2950.	85.0	47.9	10.3	6.4-13.7	.186	12.6
CL	PRE	10	94	16.0	5-42	.740	44.9	1736.	512.5-3763.	68.4	38.2	9.1	6.0-12.9	.136	14.5
CFL	PRE*	5	44	13.3	5-22	.748	37.2	1493.	512.5-2738.	85.2	37.9	9.0	7.2-11.0	.156	11.5
CFL	POST		46	12.4	6-21	.540	29.6	1231.	662.5-2350.	54.7	30.1	10.1	7.5-13.6	.191	12.8

Abbreviations: same as for Table XI

TABLE XIII. STRESS AND RIVALRY CHIRP RATES OF
LEPERISINUS OREGONUS AND L. CALIFORNICUS

SP- YR	SITU	n	n	No. of chirps per second		
				Mean	Range	S.E. C.V.
OR	STR	4	40	7.14	1.5-11.5	.441 39.1
OR	RIV	3	30	4.02	1.5- 6.0	.200 27.2
CFL	STR	6	60	4.14	0.5- 7.5	.213 29.8
CL	RIV	1	10	3.25	1.5- 4.0	.227 22.1

Abbreviations: same as for Table XI

the abdominal tip, so could be called a "double chirp" (Rudinsky, verbal communication), "diplosyllable" (Broughton, 1963) or "phonatome" (Morris and Walker, 1976 citing Leroy and applied to wing motion of Orthoptera). For L. oregonus and L. californicus, it was not determined which direction produces a major chirp and which produces a minor chirp. It was not possible to decide whether a given major chirp should be paired with the following or with the preceding minor chirp.

In stress and rivalry situations, males produced a nearly continuous run of ungrouped, "single" (as opposed to double) chirps. In the latter part of most recordings, chirping was less regular and frequent than near the beginning of the sound emission. Single chirp toothstrikes were mostly below the baseline, and each toothstrike's largest excursion away from and back to the baseline was down and then up, on our apparatus (Plate VII C, F; Plate VIII C, F), as in major chirps. In Dendroctonus pseudotsugae (Rudinsky and Ryker, 1976), similar "simple" (as opposed to "interrupted") chirps are produced during a downward, backward abdominal motion, and the silence between chirps occurs during a retraction of the seventh tergite in an upward, forward abdominal motion.

Oscillograms were also taken of some uncommonly produced sounds of L. oregonus males (Plate IV B, D, E; Plate IX A-D; Plate XI A-H) and L. californicus males (Plate IV I, K; Plate X A-E; Plate XII A-H; Plate XIII A-I). Descriptive statistics and comparisons of uncommon chirps with common chirps of the same males are tabulated in the Appendix along with results for typical sounds tabulated by individual males.

Newly captured beetles stress-chirped more readily than those which had been refrigerated. Without acoustic equipment, stress stridulation was audible only when a beetle was held to the ear. Among 25 recently trapped L. californicus heard stridulating in the field, 15 made stress chirps ranging from very soft to loud and from very few to almost continuous and super-fast. I had to place my ear practically on the log to hear two L. oregonus stridulating as they followed their females further into gallery arms being excised. One made loud, short series and the other made soft, long series.

Carrier frequency

The frequency spectra were wide in four recordings analyzed on the sona-graph. They ranged from below one kHz to 18 kHz but mostly below 15 kHz for L. californicus stress chirps, to 18 kHz for L. californicus major chirps, to 14-15 kHz for L. californicus minor chirps, to slightly over 16 kHz for L. oregonus stress chirps, and to 14 kHz or occasionally 22 kHz for L. oregonus major and minor chirps. No bands of maximum intensity were apparent. The carrier frequency ranges much higher than the toothstrike rate. When the distance between first and second waves within one of the large toothstrikes in Plate XI (C) is measured (.1 msec), a rate of 10 kHz is obtained, which is well within the carrier frequency range.

Comparisons using parameters measured on the oscilloscope

Any differences ($P < .05$) between species, situations and/or chirp types discussed herein occur despite variation among males within groups, which was nearly always highly significant.

(i) Stress versus rivalry

L. oregonus stress chirps did not differ from L. oregonus rivalry chirps in number of toothstrikes, duration, toothstrike rate or chirp rate. L. oregonus stress chirps did not differ from L. californicus stress chirps except in chirp rate ($.025 < P < .05$), which was three chirps per sec faster in L. oregonus. L. californicus rivalry chirps fell within the range of L. californicus stress chirps but could not be compared statistically, since only one rivalry recording was obtained for this species. Fig. 13 gives some idea of individual variation. Although the three L. californicus with unusually high toothstrike numbers had all been recently disturbed from female gallery entrances, several males of both species made the usual small chirps in similar situations.

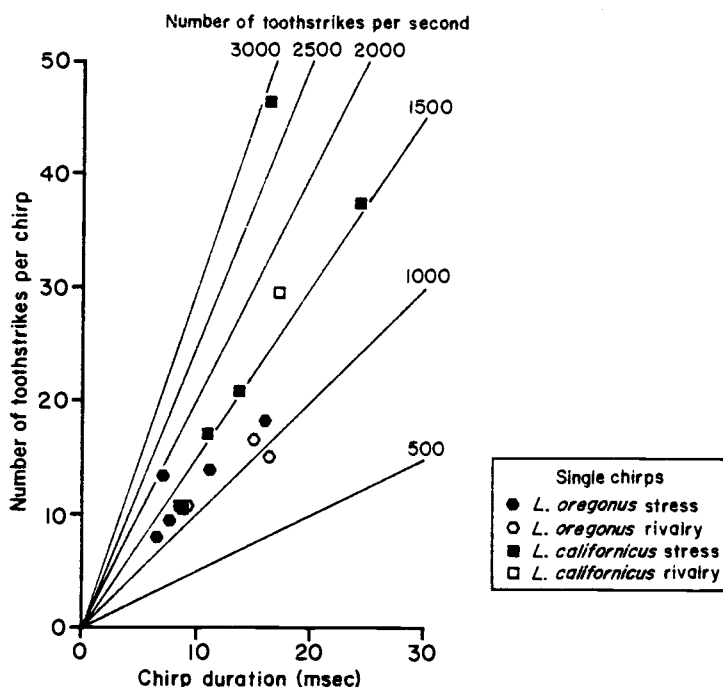


Fig. 13. Variation among males in stress and rivalry chirps. Each point corresponds to a mean of 15 chirps per male.

(ii) Major versus minor chirps

Of the 33 males recorded in premating situations, minor as well as major chirp toothstrikes had amplitudes far enough beyond the baseline to be distinguishable in 31 males. Of these, 22 conformed to the generalization that major chirps have equal numbers of toothstrikes, shorter durations and faster toothstrike rates than minor chirps of the same male. More *L. californicus* (13 of 15) than *L. oregonus* (9 of 16) conformed to this generalization. There were proportionally more nonconformers in 1975 (4 of 6 *L. oregonus*, 2 of 6 *L. californicus*) than in 1976 (3 of 10 *L. oregonus*). When each of the four species-year groups was tested separately, large and significant differences ($P < .0005$) not overruled by interaction (chirp type with male) were present between major and minor chirp durations in 1976 *L. oregonus* and 1976 *L. californicus* and between major and minor chirp toothstrike rates in these two groups and also in 1975 *L. californicus*. A significant ($P < .05$) but slight difference (3.3 toothstrikes) was present between major and minor chirps of 1976 *L. californicus*, but is within measurement error that can

occur when determining the beginning or end of a chirp. Every male had at least one difference between major and minor chirps. All but two of the 31 males conformed to the generalization with respect to at least one variable.

Mechanically, the differences probably result from a more rapid movement of the scraper across the file in one direction than in the opposite direction. During analysis of over 1500 chirps, it was noted that chirps with high toothstrike rates sounded "squeakier" than chirps with low toothstrike rates. It is not known whether this "pitch of the envelope" is as perceptible (at full speed) to Leperisinus spp. as it is (at quarter speed) to the human listener.

(iii) Differences in premating stridulation between and within species

There were significant differences ($P < .005$ or $P < .0005$) between the four species-year groups (1975 and 1976 L. oregonus and L. californicus) in all variables except major chirp toothstrike rate. Figs. 14 (top), 15 (top) and 16 (top) show results of Student-Newman-Keuls multiple comparison tests ($P = .05$) among these groups for series, major chirps and minor chirps, respectively. Figs. 13 (bottom), 14 (bottom) and 15 (bottom) give some idea of individual variation as well as overlap among groups.

The most appreciable species difference was that L. oregonus stridulated faster than L. californicus by about eight chirps per sec. Duration of the L. californicus series was longer than that of L. oregonus by about 900 msec. Number of chirps per series did not differentiate between species, since 1976 L. californicus had more chirps per series than L. oregonus but 1975 L. californicus were intermediate. In both major and minor chirps, L. californicus had more toothstrikes than L. oregonus but there was overlap. No L. oregonus produced chirps with over 100 toothstrikes, whereas nine of 15 L. californicus did so. Major chirp durations did not differentiate between species, since 1976 L. californicus had longer major chirps than L. oregonus but 1975 L. californicus were intermediate. Minor chirps were longer in L. californicus than in L. oregonus. Toothstrike rates did not separate the species.

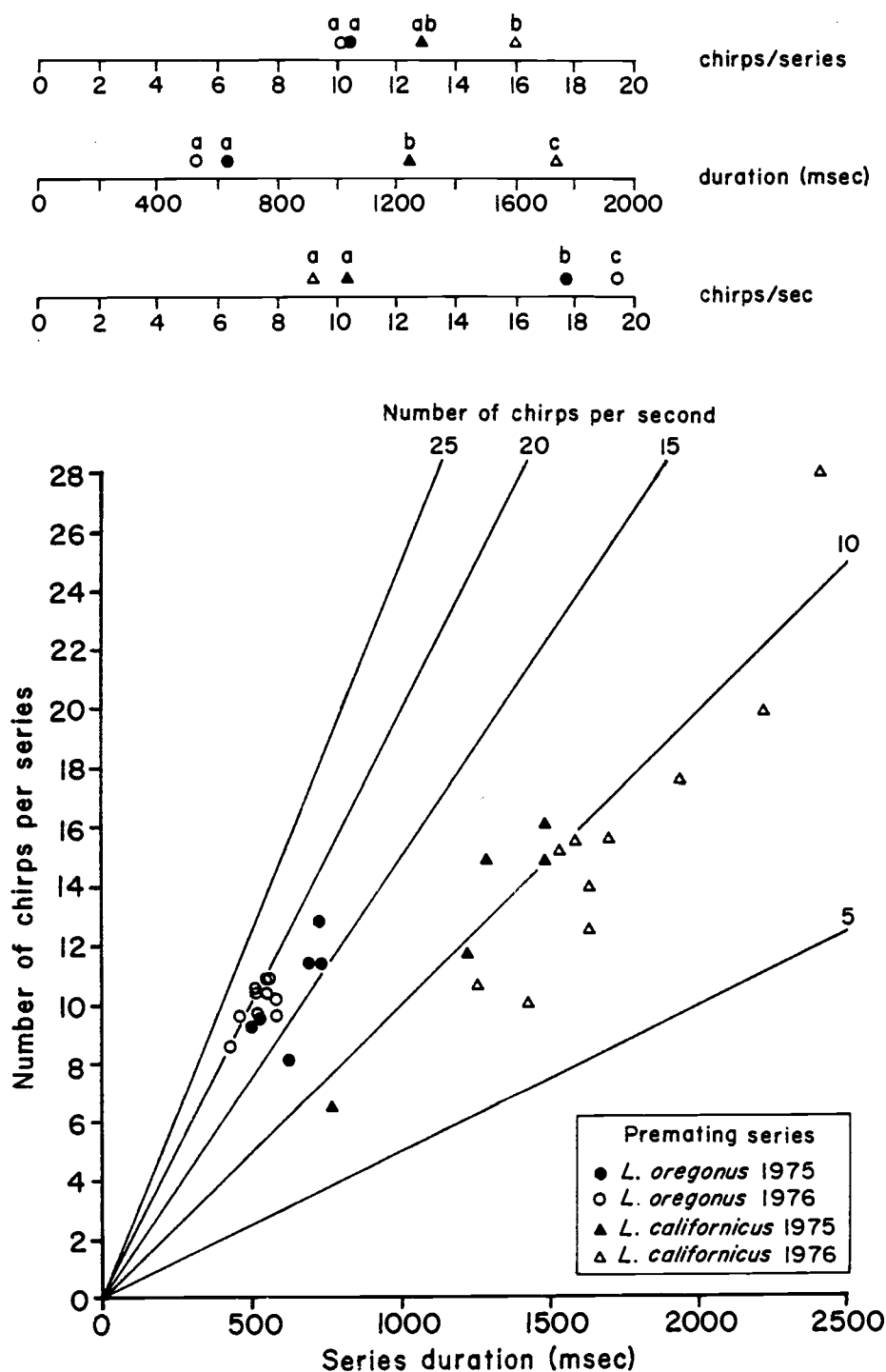


Fig. 14. Premating series: differences among species-year groups using Student-Newman-Keuls multiple comparison tests, with each point corresponding to a group mean (top); variation among males, with each point corresponding to the mean of 5-10 series of a male (bottom).

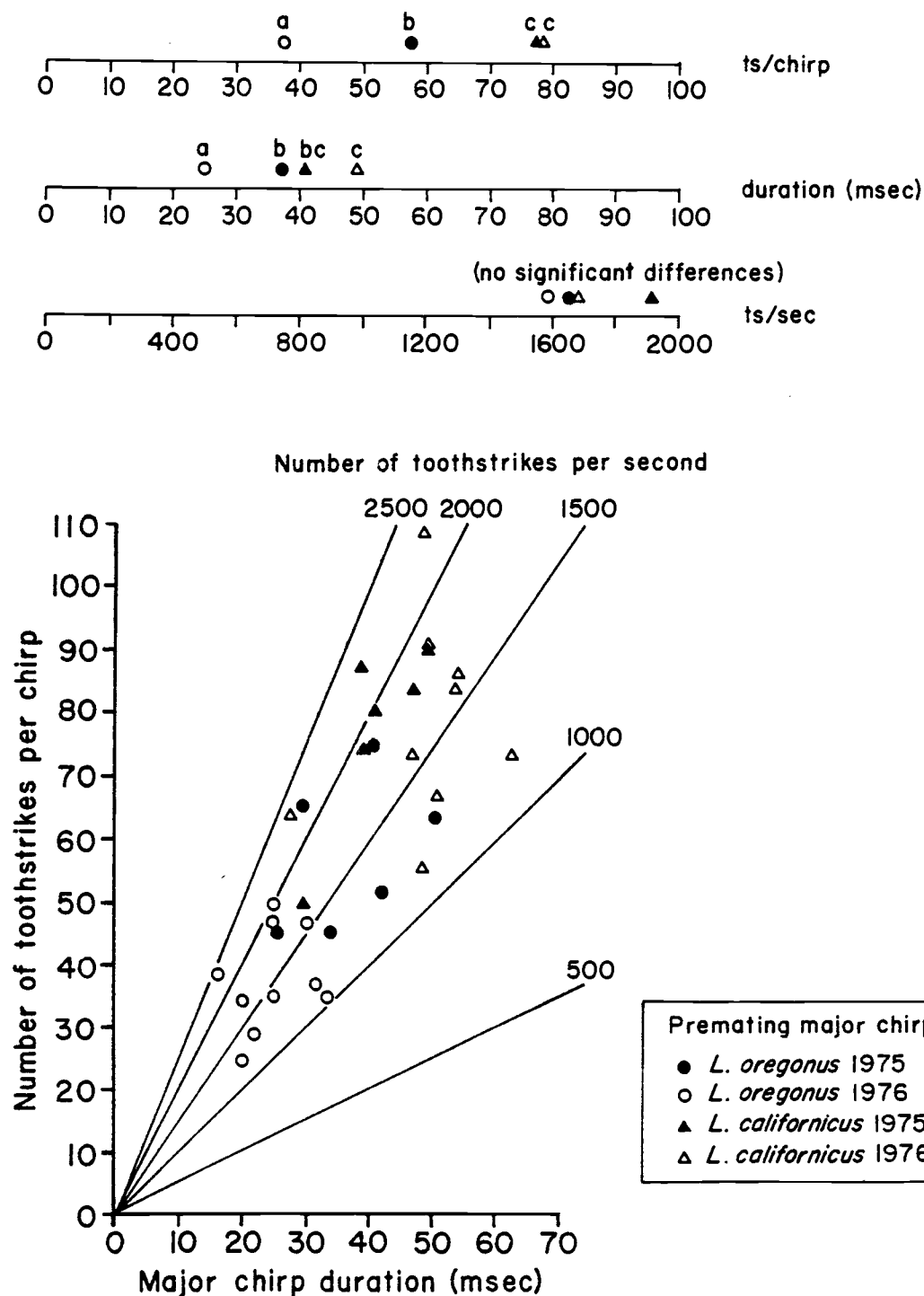


Fig. 15. Premating major chirps: differences among species-year groups using Student-Newman-Keuls multiple comparison tests, with each point corresponding to a group mean (top); variation among males, with each point corresponding to the mean of 15 major chirps of a male (bottom).

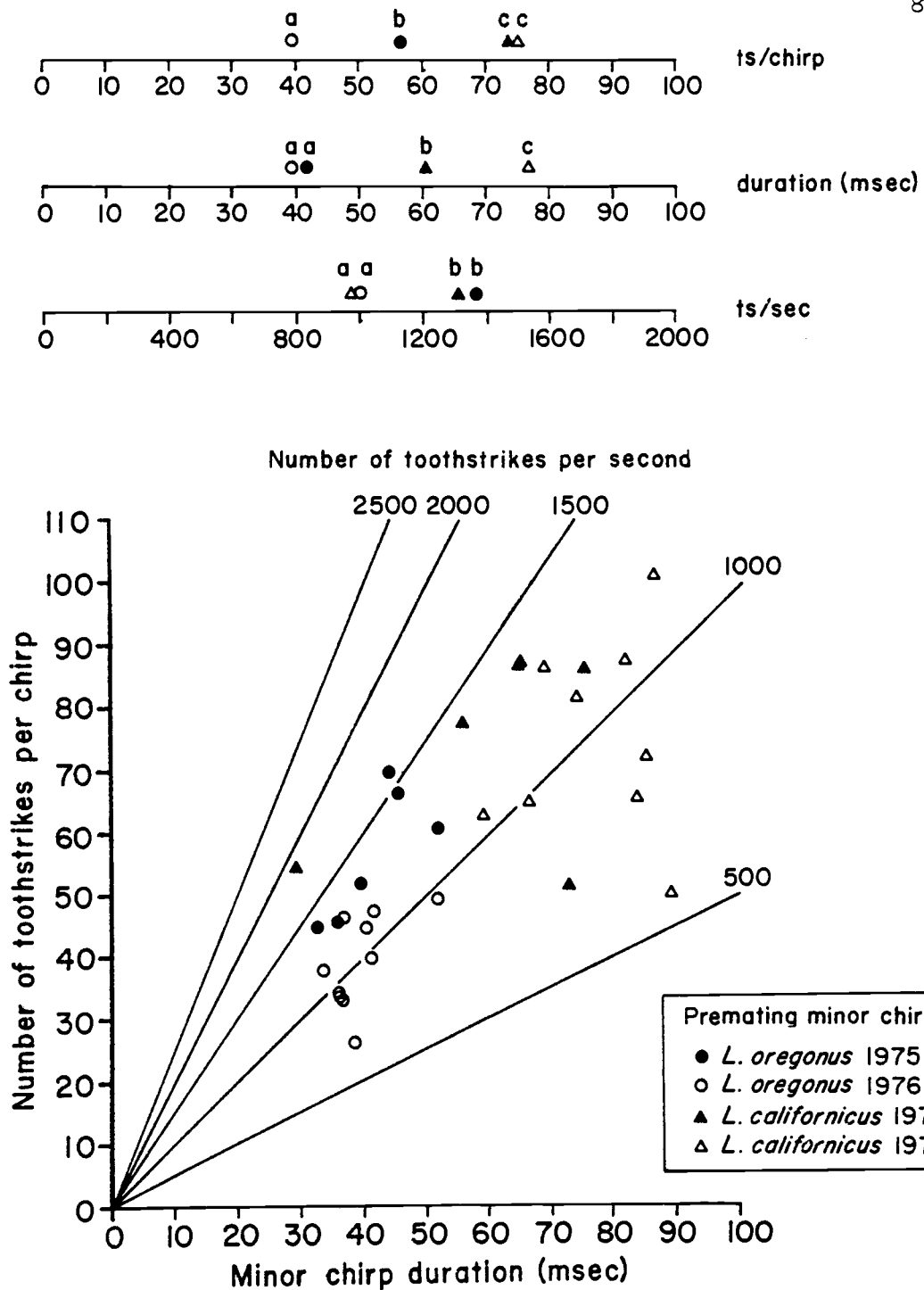


Fig. 16. Premating minor chirps: differences among species-year groups using Student-Newman-Keuls multiple comparison tests, with each point corresponding to a group mean (top); variation among males, with each point corresponding to the mean of 15 minor chirps of a male (bottom).

Differences between years, in minor chirp toothstrike rate, or between years within species, such as the fewer toothstrikes and shorter major chirp duration of L. oregonus in 1976 than in 1975, are not readily explained. The 1976 L. oregonus were excised from overwintering burrows, did not get "flight exercise" and were of maturity near the minimum found in naturally attacking conspecific beetles. However, the males' premating behavior at female gallery entrances seemed straightforward, and all but one pair (introduced into a bad spot in the bark not apparent at the surface) produced larval progeny as did the 1975 L. oregonus. Since beetles of both species were used within several days after capture in 1976 but spent quite some time in the refrigerator in 1975, the 1976 beetles were probably in better physiological condition. However, behavior of males which stridulated at female gallery entrances was similar in both years.

The most unambiguous species difference was in chirp rate, with no L. oregonus males' means overlapping with L. californicus males' means and only two L. oregonus males' (one unusual) ranges overlapping with two and three L. californicus males' ranges. It is doubtful that temperature differences alone, which varied from 24-28°C on the night when the fairly uniform 1976 L. oregonus were recorded, would have caused the species difference in chirp rate which occurred in both years.

(iv) Stress plus rivalry versus premating

Within each species, stress and rivalry chirps had fewer toothstrikes and shorter durations than either major or minor premating chirps of either year. The toothstrike rate of these single chirps was not different from that of major chirps. The toothstrike rate was faster in L. oregonus single chirps than in 1976 L. oregonus minor chirps, but not faster than in 1975 L. oregonus minor chirps. The toothstrike rate of L. californicus single chirps was not different from minor chirps of L. californicus recorded either year.

(v) Premating versus postmating

No consistent differences or significant differences not overruled by interaction (situation with male) occurred between premating and postmating chirps of five L. californicus males which made sufficient numbers of both for sampling. There were consistent (four out of five males) and significant differences between premating and postmating series durations ($P < .025$) and especially chirp rates ($P < .0005$). It is difficult to suggest why a male would make slightly shorter series (about 260 msec) and chirp slightly faster (1.1 chirp per sec) after mating than before. Not enough males (four) did this to warrant speculation.

Proportion of sound during stridulation

The proportion of sound, as compared with silence, produced while the male was actually chirping was estimated using mean values for each male in the following equations:

$$\text{In stress and rivalry, percent sound} = 100 \times .001(\text{msec per chirp})(\text{chirps per sec})$$

$$\text{In premating, percent sound} = 100 \times .5(\text{msec per major chirp} + \text{msec per minor chirp}) \times (\text{chirps per series}) / (\text{msec per series})$$

No statistical comparisons were done, since these values are calculated from averages rather than random variables. From the results in Table XIV, it appears that premating series have a higher proportion of sound than continuous runs of single chirps, so are "fuller" sound patterns.

TABLE XIV. PROPORTION OF SOUND PRODUCED DURING STRIDULATION

Species	Situation	Number of males	Percent sound	
			Mean	Range
<u>L. oregonus</u>	stress (1975)	4	6.8	4.1- 9.0
	rivalry (1975)	3	5.2	4.5- 6.4
	premating (1975)	6	64.2	57.7-71.0
	premating (1976)	10	61.5	50.5-66.3
<u>L. californicus</u>	stress (1975-76)	6	5.7	1.9- 9.1
	rivalry (1976)	1	5.6	
	premating (1975)	5	51.7	29.3-65.9
	premating (1976)	9	56.0	37.0-72.0

If silences and scratching between series were taken into consideration, the proportion of sound during premating would be very low. A male producing series lasting one sec with 50 percent sound would produce only 20 percent sound if chirping frequently, at 24 series per min, and only five percent sound if chirping occasionally, at six series per min. However, it is reasonable to consider what is happening while the male is chirping rather than while he is not. Chirps in premating series are longer than those produced during stress or rivalry, and minor premating chirps fill in gaps between successive major chirps.

Relationships among variables within males

The number of toothstrikes per chirp usually increased together with chirp duration, and the number of chirps per series usually increased together with series duration. Simple linear regressions, using numbers as dependent variables and durations as independent variables, were significant for most chirp types of most males in most behavioral situations (Table XV). See the Appendix for slopes and R^2 values.

TABLE XV. PROPORTION OF SIGNIFICANT REGRESSIONS OF NUMBERS ON DURATIONS

Situation	Sound	L. oregonus			L. californicus		
		No. of males	Percent significant at:		No. of males	Percent significant at:	
			.05	.0005		.05	.0005
Premating	major chirp	17	82	53	16	94	38
	minor chirp	16	94	63	15	87	53
	series	17	100	71	14	100	100
Postmating	major chirp	0	—	—	7	71	43
	minor chirp	0	—	—	6	100	67
	series	0	—	—	5	100	100
Stress	single chirp	5	80	80	6	100	67
Rivalry	single chirp	3	100	67	1	100	0

Toothstrike rates and chirp rates usually had lower coefficients of variation for individual males as well as higher F-values for variation among males within species, year, situation or chirp type groups in comparison with values of corresponding statistics for numbers (of

toothstrikes or chirps) and durations (of chirps or series). This simply indicates that rates are individual characteristics.

Atypical stridulation

Atypical sound emissions were photographed and, where possible, measured. This was essentially "just for the record," in case they should appear and perhaps be more common in Leperisinus spp. or in related genera, such as Hylesinus, studied in the future.

A few L. oregonus produced "double chirps," with a minor component closely following the major one, during stress (Plate IV B) and rivalry (Plate IV D). Examination of the former (Plate IX A-D) shows that they occurred sporadically, and that the difference between major and minor toothstrike forms was the same as in premating.

One L. californicus made very soft "extra" minor-type chirps (Plate X A-E) midway between consecutive stress chirps during part of his sound emission. They could not be paired with the preceding, as opposed to the following, major-type chirp. This male had been disturbed from a female gallery entrance just before being hand held for stress recording so may have experienced a confusion of stimuli. However, he was the only male that produced detectable minor-type chirps in such a situation. His stress chirps were large (in toothstrike number), but his premating and postmating chirps (recorded three days later) were much larger.

Two L. oregonus and one L. californicus "skipped" some chirps in premating series. Of the L. oregonus, one skipped them entirely in just a few series so produced series with fewer, non-alternating chirps (Plate IV E; Plate XI A-C). The other produced series with minor chirps soft near the beginning and non-detectable near the end (Plate XI D-H) throughout the recording. Both gained admission to female galleries. One L. californicus, which mated, infrequently skipped chirps.

Hesitations (Plate XII A) occurred during premating and/or postmating series in five L. californicus, two of which mated. At least three of these males also interrupted the pattern of alternating major and minor chirps by making low spike rate chirps, onomatopoeically

Oscillograms of L. oregonus and L. californicus male stridulation - II

- Plate IX L. oregonus, occasional double stress chirp production. (A) many successive stress chirps, including five double and one extra, (B) one double chirp, with major and minor components close together, (C) toothstrikes in major component, (D) toothstrikes in minor component. Legend: dc, double chirp, e, extra chirp.
- Plate X L. californicus, atypical stress stridulation. (A) many successive stress chirps, with extra minor-type chirps between the usual major-type chirps and audible in the right (latter) half of the photo, (B) major-type stress chirp, ninth after the scratching sounds, (C) minor-type extra chirp, tenth after the scratching sounds, (D) toothstrikes in major-type chirp, (E) toothstrikes in minor-type chirp. Legend: scr, scratching sound.
- Plate XI L. oregonus, atypical premating stridulation. Male which totally skipped alternate chirps in three series (A) one series, (B) second chirp in Fig. A, (C) toothstrikes in chirp of Fig. B; male which skipped minor chirps near end of most series (D) one series, (E) major chirp, first in Fig. D, (F) soft minor chirp, second in Fig. D, (G) toothstrikes in major chirp, (H) toothstrikes in minor chirp. Legend: sln, silence in place of minor chirp.
- Plate XII L. californicus, atypical premating stridulation of one male. (A) one series with three unusually long hesitations (.125-.375 sec) between consecutive chirps, (B) part of a different series with several "crunchy" sounding (at quarter speed) chirps, (C-H) chirps of the series in Fig. B. Legend: cr, crunchy chirp; maj, major chirp; min, minor chirp; scr, scratching sound.
- Plate XIII L. californicus, atypical chirps. First male (A) several "clucks" which occurred between premating series, (B) one cluck, (C) toothstrikes in the cluck; second male (D) one "soft" chirp, among several made between premating and post-mating production of series, (E) toothstrikes in the soft chirp; third male (F) four "weird" chirps, each preceded by two scratching sounds; (G) the fourth scratch-scratch-chirp group of Fig. F, (H) the chirp of Fig. G, (I) toothstrikes of the chirp of Figs. G-H. Legend: ch, chirp; ck, cluck; scr, scratching sound; sln, silence after scratching sounds preceding "weird" chirp.

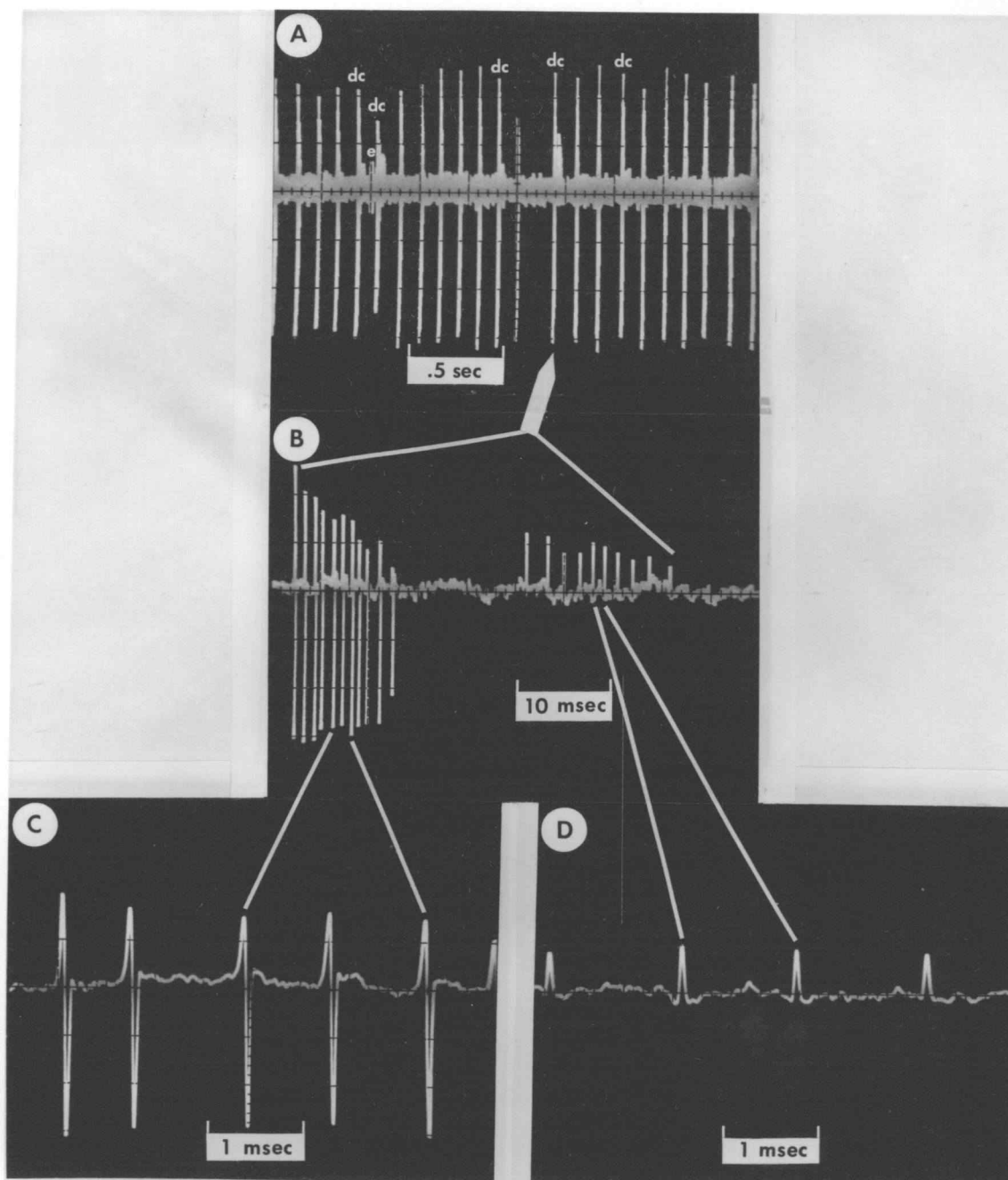


Plate IX

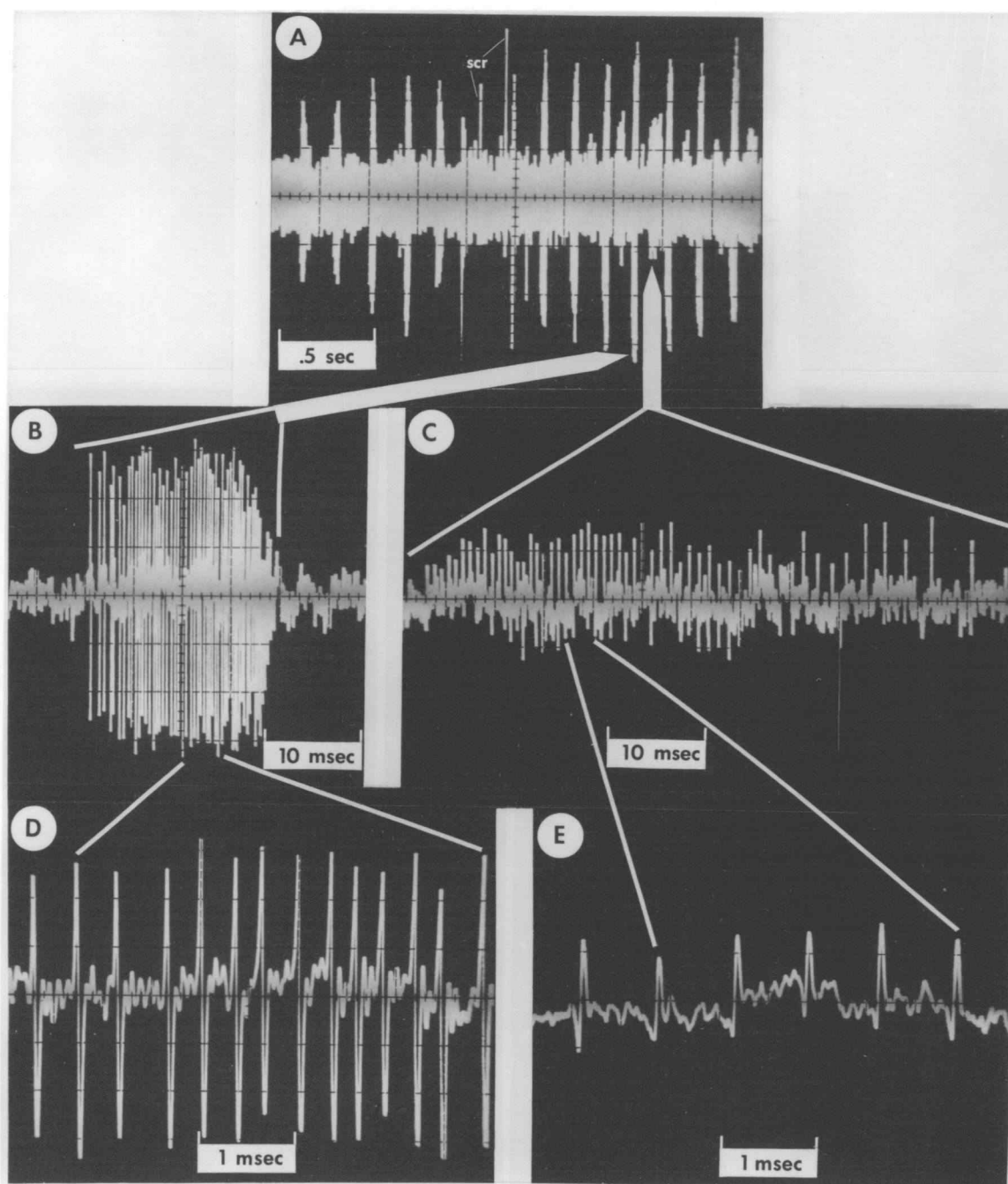


Plate X

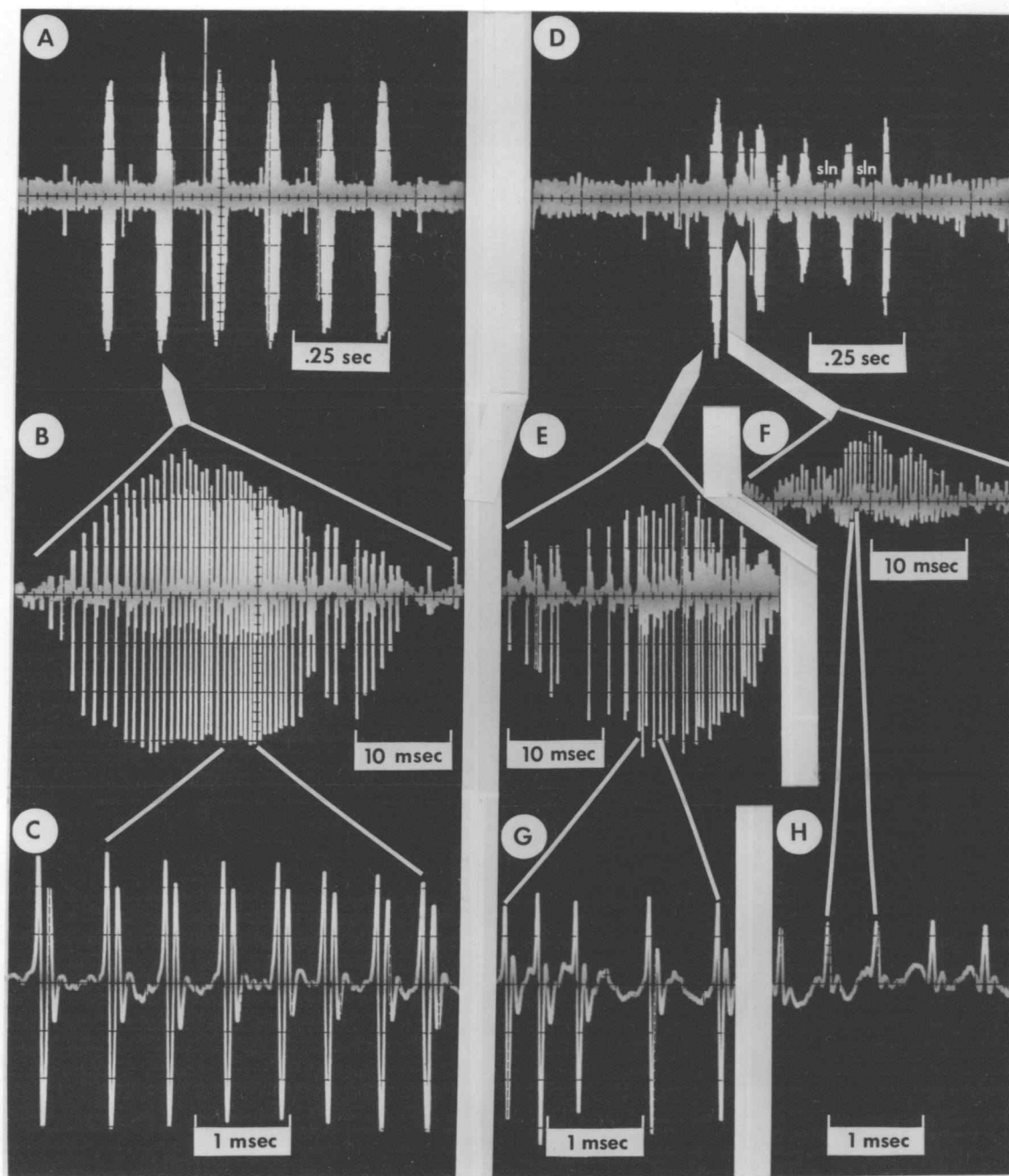


Plate XI

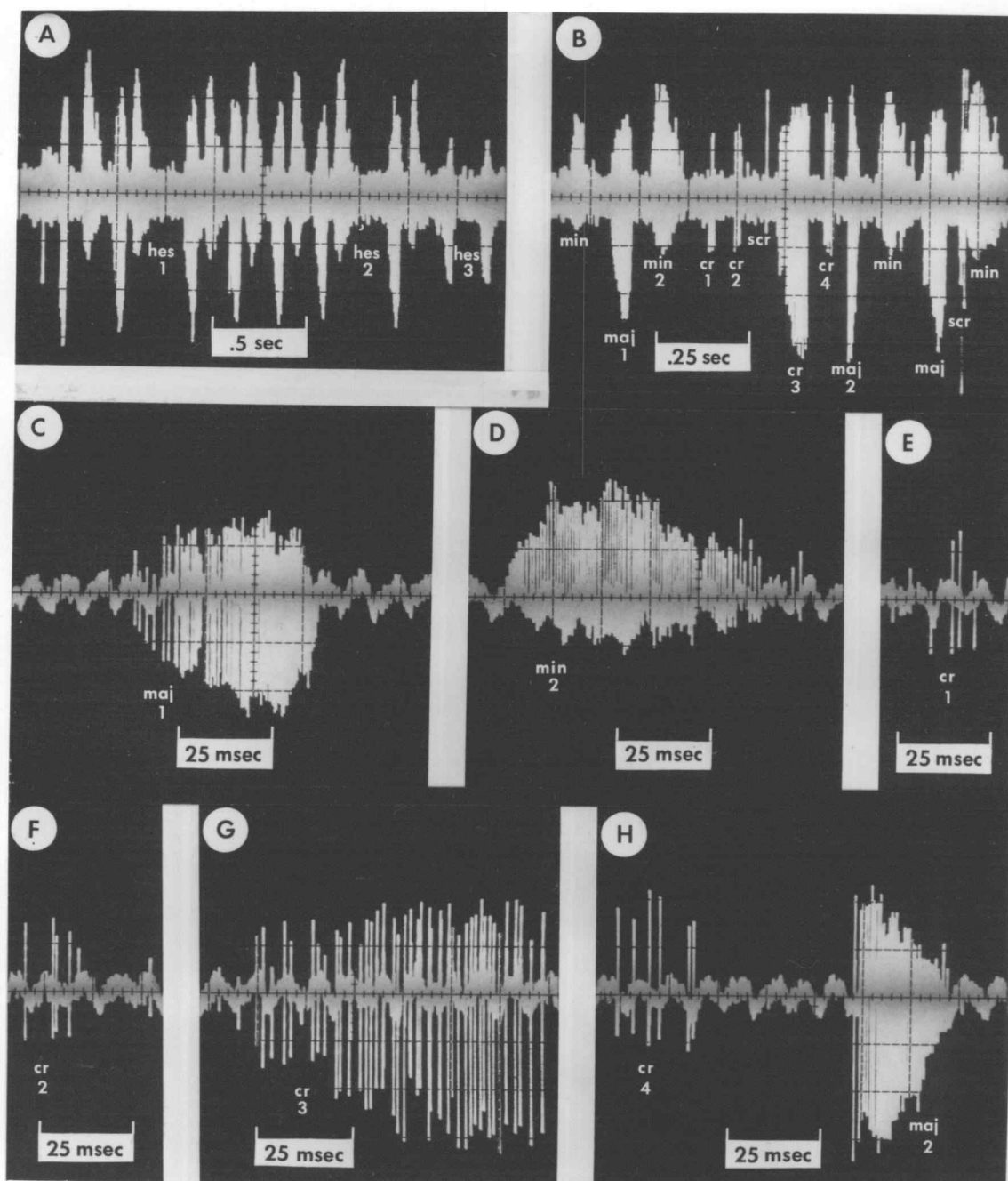


Plate XII

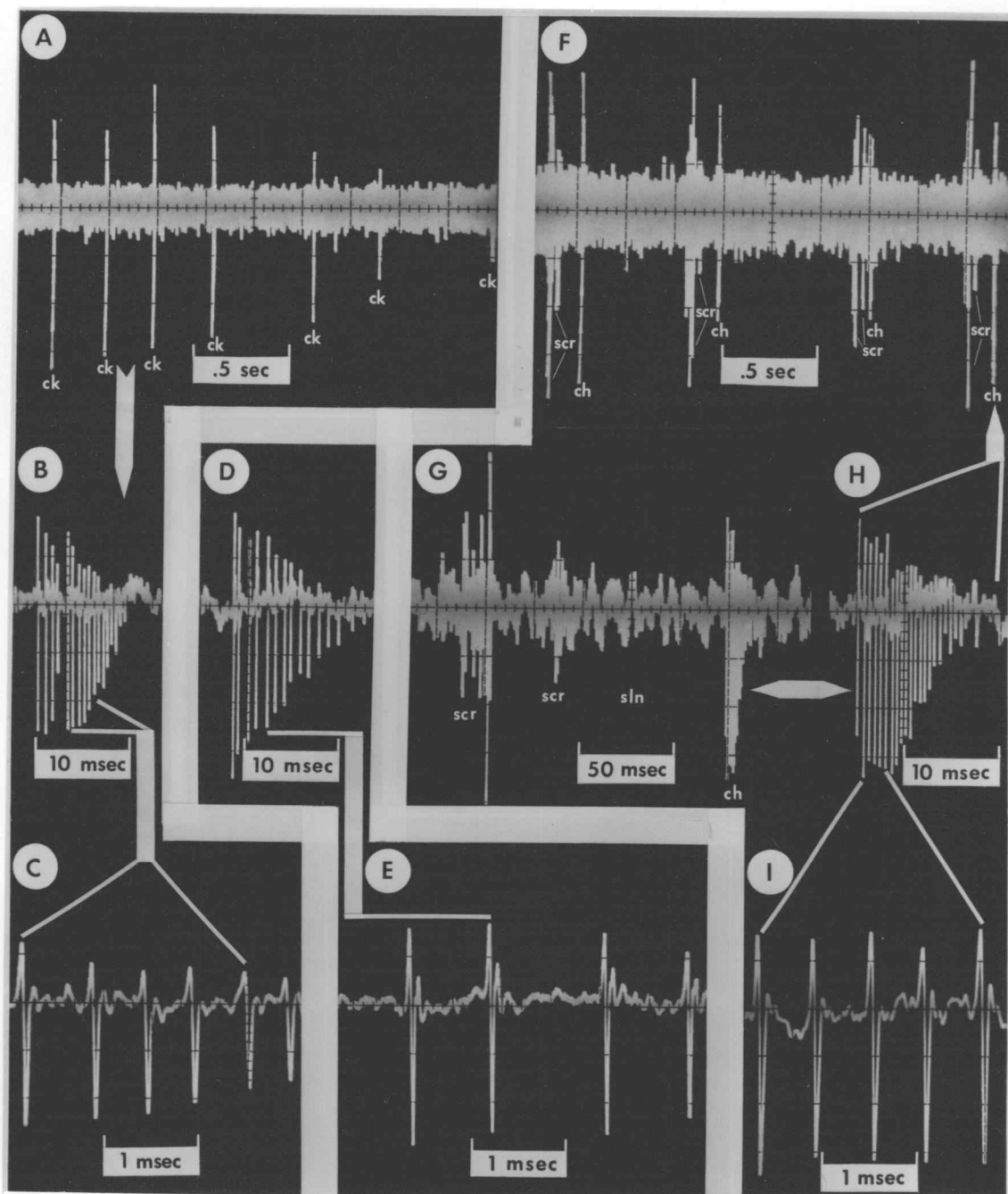


Plate XIII

labeled "crunches" (Plate IV K; Plate XII B, E-H), which were not nearly as dense as typical chirps in the same series (Plate XII B-D, H).

Short, ungrouped chirps were made by some L. californicus males at female gallery entrances. The "clucks" (at least 50)(Plate XIII A-C) were made between premating series, including during an attempt to mount the female. The "soft" chirps (about 20)(Plate XIII D-E) were made between premating and postmating stridulation, after the male had been silent and apparently in mating position, then changed his position but remained with his abdomen over the gallery entrance. Both males may have encountered difficulties with their respective females. A few other males (not recorded) occasionally made short, ungrouped chirps in premating situations. The "weird" chirps (Plate XIII F-I) seem to be incidental sounds resulting from a bounce of the male's abdomen against his elytra. Each occurred about 75 msec after a quick, double-scratching noise during a jerk of the male's body. They were interspersed with two series and began after typical stridulation had tapered off.

Some Leperisinus males produced typical premating-type series in uncommon situations. If two males stridulated at the same female gallery simultaneously, or one was present while the other was stridulating, the situation was designated "contest" to differentiate it from premating. However, they probably were not competing by stridulating but simply producing premating series in the presence of a female and, incidentally, another male. Both species did this, but only two L. californicus were sampled (in parts of the recordings where it was ascertained that only one male was stridulating). When one L. oregonus male made typical premating-type series while entering an abandoned female gallery already occupied by another male (both confirmed by dissection) which had there a few min earlier, the situation was designated as "odd."

The meaning, if any, of atypical chirps and series or atypical situations is unknown. However, we also do not know what stimuli elicit typical stress, rivalry (defense? aggression?), premating and postmating stridulation. In a discussion of sound production which does not claim to explain communicative function, it seems legitimate to report the

variety of sounds which these insects emit.

Comparisons with other species

Mention will be made only of species whose sounds have been photographed or measured. Since behavioral contexts were discussed in the introduction, emphasis is now being placed on sound structure.

Series of two types of alternating chirps have been found in Leperisinus fraxini, some of which produce them during premating, and in Hylesinus oleiperda, which produces them during stress as well (Rudinsky and Vallo, in press). Visual comparisons of my data with means for L. fraxini chirps indicate that its stress, rivalry and single premating chirps are similar to those of L. oregonus and, more so, L. californicus. The louder of two alternating types of L. fraxini premating chirps is within the range of our Oregon species' premating chirps and has a toothstrike rate closer to the latter's minor chirps.

Both to- and fro- motions of the stridulatory apparatus are acoustically effective in many insects. Among scolytids, these include Pseudohylesinus nebulosus (Oester, verbal communication and oscillogram), Scolytus mali (Rudinsky and Ryker, verbal communication and oscillogram) and Ips calligraphus (Wilkinson et al., 1967). Among other Coleoptera, these include Pissodes strobi and P. approximatus, two curculionids, (Harman and Kranzler, 1969) as well as four cerambycids of subfamily Lamiinae (Finn et al., 1972). Among Orthoptera, these include the tettigoniids Metrioptera sphagnum (Morris et al., 1975), Orchelimum spp. (Morris and Walker, 1976) as well as Uhler's katydids (Amblycorpha uhleri Stål species complex) which produce four phonatome types in their calling song (Walker and Dew, 1972). Among Hymenoptera, Pogonomyrmex occidentalis (Formicidae) produces higher intensity chirps during the upstroke than during the downstroke of the gaster (Spangler, 1967). This alternation of sound intensities in correspondence with stridulatory motions also occurs in Orchelimum spp. (Morris and Walker, 1976) and Leperisinus.

Insects have other ways to vary their sound. Hylurgops rugipennis (Scolytidae) produces a bimodal pattern of slow followed by faster

chirps (Oester, Ryker and Rudinsky, in press). Dendroctonus spp. (Scolytidae) produce "interrupted" chirps, containing two to six subchirps separated by brief gaps, as well as "simple" chirps. Measurements of male chirps have been reported for D. pseudotsugae (Michael and Rudinsky, 1972; Rudinsky and Ryker, 1976), D. ponderosae (Michael and Rudinsky, 1972; Ryker and Rudinsky, 1976b), D. rufipennis, D. brevicomis and D. frontalis (Rudinsky and Michael, 1974) and D. valens (Ryker and Rudinsky, 1976a). In general, these Dendroctonus have chirps of longer duration than Leperisinus, their maximum number of toothstrikes (84 in D. pseudotsugae) is less than in L. californicus, and their maximum toothstrike rate (1816 per sec in D. brevicomis) is considerably slower than in major chirps of either L. oregonus or L. californicus. The ant, Pogonomyrmex occidentalis, can also produce both simple and interrupted chirps (Spangler, 1967). In 12 Berosus spp. (Coleoptera: Hydrophilidae), chirps are produced erratically during stress but in evenly spaced tremulos during premating (Van Tassell, 1965). In three Tropisternus spp. (Hydrophilidae), the variety of sound includes dense chirps, very low pulse rate (under 65 per sec) buzzes, trills and slow trills (about 8 and 3 chirps per sec, respectively), and ticking phrases (groups of brief sounds)(Ryker, 1976).

The rate of to- and fro- stridulatory motion can get very high in Orchelimum spp. (Morris and Walker, 1976). When individual phonatomes (produced by one cycle of wing movement) occur at 90 per sec in O. vulgare, they are not distinguishable to the human ear, so a sequence of phonatomes is heard as a single sound described as a "buzz mode" (ibid). Phonatomes are distinguishable when produced at lower rates in "tick" modes, and intermediate rates produce "rattle" modes (ibid). Insects can probably resolve sound patterns more finely than can humans (Haskell, 1961), but our descriptive terminology is necessarily based on human abilities.

"Ultrasonic modes" (33 kHz) alternate with "audio modes" (15-20 kHz) in Metrioptera sphagnorum calling songs (Morris et al., 1975) and are produced by different stroking techniques over different regions of the file (Morris and Pipher, 1972). Waves correspond to file teeth

struck, follow one another before decay can set in, and have a repetition rate equal to the carrier frequency in this katydid (ibid).

Although Leperisinus may produce ultrasonic sounds to which our equipment is not sensitive, I have never seen the males making stridulatory motions near our microphone without hearing them chirp at the same time. Hand held female Leperisinus often snap their abdominal tip back under the elytra after moving it outward a short distance, but whether they produce sound (very soft, or ultrasonic) by this motion is not known.

The pulse structure of some scolytids does not show as rapid a wave decay rate as in Leperisinus toothstrikes. Ips concinnus (Oester, 1977) has several more or less equal waves per pulse.

It seems that Leperisinus, with only two distinct sound patterns, produces only a small part of the range of stridulations reported in insects so far.

V. DISCUSSION

In the vicinity of Corvallis, Oregon, Leperisinus oregonus and L. californicus can be found breeding in the same pieces of felled Fraxinus latifolia (Oregon ash). Their attack times overlap, both species are monogamous, and they are of similar size. The female initiates a gallery and is joined by a male which usually stridulates at the entrance. Since no hybrid pairs were found in excised galleries, members of these sympatric Leperisinus species presumably can recognize conspecifics by using olfactory, visual, tactile and/or auditory cues. In addition, other information may be transferred via these media.

The stimulus for male premating stridulation has not been established in this study. The term "attractant chirp" (Rudinsky and Ryker, 1976) is used for sounds emitted by Dendroctonus pseudotsugae in response to female frass or synthetic attractants as well as to females in logs (Michael and Rudinsky, 1972). It has not yet been proven an appropriate term for L. oregonus and L. californicus. In these two species, the male locates the female gallery, digs in the frass, attempts to enter and/or makes tactile contact with the female before stridulating. The fact that he often waits several minutes before chirping, or even spends a long initial period silently removing frass from the gallery, suggests that he has already identified the female as conspecific. Otherwise, he would be wasting time, expending energy and incurring risk of predation (if stridulating on the bark surface), with no assurance that this behavior would enable him to reproduce.

Tactile behavior did not seem sufficiently different during early stages of pairing to function in species identification, but females were mostly below the bark surface and therefore difficult to observe.

The possible role of visual cues in close range species identification was not investigated for L. oregonus and L. californicus.

Females may emit sounds which our equipment was unable to detect. However, unless Leperisinus is highly sensitive to low intensities, or perhaps to ultrasonic frequencies, female acoustic signals would only be effective over short distances, to beetles walking near the entrance

on the same log. The function of a "calling" signal is probably performed by an unidentified pheromone which aggregates the species to the host and attracts males to female galleries.

The function of Leperisinus male premating stridulation has not been ascertained. It may combine with tactile efforts and perhaps chemical emissions to facilitate "pair formation" by overcoming female resistance to a male entering her gallery. The term "courtship" is reserved for signals "occurring after pair formation and culminating in copulation or insemination when the courted individual is sexually responsive" (Alexander, 1967). Premating stridulation was followed by copulation, so may have served a courtship function, in about half the L. californicus pairs observed. However, the same sound pattern (series of alternating major and minor chirps) was produced by other L. californicus and by L. oregonus which entered the gallery and disappeared from view, under bark, before mating. This sound pattern was also produced in the postmating situation by L. californicus males at gallery entrances. Only a few males mated and/or entered without being noted to stridulate, and some of these were observed only visually. Studies with surgically silenced males would determine whether stridulation is a necessary prelude to copulation and/or gallery entry. When produced less frequently, in the gallery, during feeding and excavation, these series of chirps may serve as pair-maintaining signals or be incidental (Barr, 1969). Chirping may again become frequent prior to in-gallery mating, but use of "bark sandwiches" (Reid, 1958; Rudinsky and Ryker, 1976) would be required to test this prediction.

There were interspecific differences in premating stridulation. L. oregonus males usually had faster chirp rates, shorter series durations, fewer toothstrikes per major or minor chirp, and shorter minor chirp durations than L. californicus males. The extent to which these differences depend on temperature is not known for these species, but recordings were made within a temperature range common during afternoon flight attack. It is not known whether female Leperisinus can perceive these interspecific differences, but "apparently, most insects select good time resolution of their hearing organs" (Michelsen and Nocke, 1974), as opposed to frequency or intensity resolution. The

distance, either through air or bark, over which females can perceive male stridulation is not known. On a log colonized sparsely, or mainly by one species, a female may never hear males of the other Leperisinus species. If males stridulate only at conspecific galleries, a female might hear congeneric beetles chirping at neighboring galleries but never need to identify and eject a male of the "wrong" species from her own. However, premating stridulation parameters may have to fall within a certain range, and accompany certain tactile and olfactory cues, to "assure" the female that a male is conspecific. Since song is a "genetic feature" (DuMortier, 1963b), premating stridulation may be just one more species characteristic.

Micro-anatomical measurements revealed quantitative interspecific differences between L. oregonus and L. californicus male acoustic organs that are more clear cut than differences between premating stridulation. Elytral lengths were correlated with file lengths, but would not completely account for wider interspecific differences in the latter. Length of the pygidium (eighth tergite in male Hylesininae) was not measured, but would probably be correlated with file length. Recent examination (during sexing) suggests that this sclerite is shorter in L. californicus (see also Plate III A-B).

The implication of the term "toothstrike," that one such event on the oscilloscope results from one file ridge being struck by the plectrum, has not been verified. However, the number of toothstrikes per chirp does not exceed the number of ridges per file in either Leperisinus species. If there is a one-to-one correspondence between file ridges and toothstrikes, the following two suggestions may be made. Since both species produce chirps with similar toothstrike rates, perhaps L. oregonus compensates for its more widely spaced ridges by stridulating more rapidly. Since L. californicus has more ridges per mm, perhaps it can produce chirps with more toothstrikes than L. oregonus while sweeping across the same length of file.

Right files are narrower than left files and may be vestigial. The suggestion that only left files are struck by left scrapers is based on use of width measurements and awaits experimental verification.

Female files have fewer ridges than male files. Since females lack scrapers, they either do not use these files or strike them in some other way. Further attempts could be made to elicit female sounds, such as those reported in Dendroctonus spp. (Rudinsky and Michael, 1973; Ryker and Rudinsky, 1976a and 1976b).

In Leperisinus males, the pattern of premating and postmating stridulation is qualitatively different from the continuous run of short chirps produced in stress and "rivalry" situations. DuMortier (1963b) regards "protest" sound (= our "stress") as a displacement activity, with stridulatory movements serving as an outlet for "intense nervous discharges in the animal" for which there are "no longer any readily available effectors" as long as the animal is captured or cornered. He groups sound phenomena under two headings: "emission ending with the creation of a situation which satisfies a need or a tendency" and "emission associated with a 'hostile' or defensive attitude, often tending to put an end to a situation of constraint (not sought by the animal)" (ibid). In Leperisinus, perhaps the positive nature of premating and postmating situations versus the negative nature of stress and "rivalry" situations is related to the different patterns of motion and sound production. Consideration of the positive or negative nature of some "atypical" situations suggests that patterns of stridulation in these contexts also were not so anomalous.

Behavioral notes indicate that "rivalry" chirps recorded were not produced during fighting. Sound in one recording of each species was stimulated by activity of a conspecific (another male at the same female breeding gallery) so could safely be called "disturbance" sound, following DuMortier (1963b). Sound in two L. oregonus recordings may have been stimulated by actions of a Homo sapiens confirming two males together in the bark, rather than by interactions between the beetles themselves. Leperisinus males, at least L. californicus, occasionally fight vigorously, so further studies might reveal "true" rivalry chirps in this genus.

L. californicus males also seemed more aggressive than L. oregonus males in their behavior toward conspecific females during premating. However, this should not be claimed as a species difference until L.

oregonus activities immediately preceding and following mating can also be observed and quantified, probably in "bark sandwiches."

The emergence of Leperisinus from brood logs as sexually immature adults constitutes a major limitation on study of these beetles. If a maturation feeding system is devised, concentrated supplies of adults emerging from brood logs could be utilized. Research with beetles collected during breeding attack is confined to the flight season, which is short for L. oregonus, and dependent on the weather.

In the field, beetles of both species land on mesh cages enclosing ash logs infested by conspecifics, although mesh is dissimilar to ash bark surface both visually and in texture. Few land on cages with uncolonized logs or logs into which beetles have been artificially introduced but are not boring well. This suggests that the aggregant is olfactory and produced by mature beetles excavating breeding galleries.

VI. SUMMARY AND CONCLUSIONS

Leperisinus oregonus and L. californicus emerge from Fraxinus latifolia brood logs as sexually immature adults. Fortuitous finds of adults dispersed in living ash trees for overwintering and/or maturation feeding suggest that L. oregonus construct short burrows in trunks and branches, whereas L. californicus enter twig crotches, buds or even leaf axils. Reemerged parents also construct these burrows. Leperisinus females initiating breeding galleries have at least 2-5 distinct eggs per ovariole, and males joining them have enlarged seminal vesicles and accessory glands. A sizeable L. californicus spring attack occurs in the vicinity of Corvallis, Oregon in addition to previously reported (Underhill, 1951) attacks of this species in Aug. and of L. oregonus in spring. Breeding galleries of both species may be initiated as early as April, but spring flight is mainly in May and early June. Trapping of both species, on different dates, in the field to cages containing naturally infested ash logs suggested that olfactory, beetle-produced and possibly species-specific aggregants are present. Sex ratios of Leperisinus attracted to these cages were usually 1:1, for both species separately. Sex ratios at emergence were also 1:1, for both species separately. Emergence as well as attack occurs mainly on sunny, 23-33°C days between 2-6 P.M. L. oregonus emergence in Sept., 1975 varied with maximum daily temperature. Along one tree, number of attacks per m² was uniform, but emergence per m² and per gallery was lower apically, due to higher parasitism and/or greater exposure to solar radiation. L. californicus produced F-1 and F-2 generations in the greenhouse when provided with cut twigs and logs. Host response to attack sometimes involved sap flow into galleries. Hymenopterous parasites or associates obtained in meaningful numbers were braconids, Coeloides scolytivorus (Cresson) and Spathius benefactor Matthews, and pteromalids, Cheiropachus quadrum (Fabricius) and Habrocytus sp.

L. oregonus and L. californicus have elytral-abdominal tergites type acoustic organs. The pars stridens consists of two files, one on the posterior medial undersurface of each elytron. The most notable bilateral, sex and species differences were: left files wider than

right files, females with fewer file ridges than males, and L. californicus with shorter files than L. oregonus. In males, there was no overlap between left file ridge spacing of L. californicus ($\bar{x}=1.9 \mu$) and L. oregonus ($\bar{x}=3.0 \mu$). Three-variable discriminant functions can completely separate the four species-sex groups on left or right sides, although four- and five-variable discriminant functions separate them further. First principal components account for 47-68 percent of variation within species-sex-side groups and are mainly "size" measures. Second principal components are mainly "spacing" measures. Canonical correlation within species-sex groups showed left and right files to be related, with 33-59 percent redundancy. Number of ridges was correlated with file length within species-sex-side groups, even when multiple partial correlation removed the influence of elytral length. The plectrum, a pair of scrapers on the seventh tergite's posterior edge, is absent in females. In males, distance between scrapers is slightly but significantly greater in L. oregonus than in L. californicus.

In the laboratory, males of both species usually stridulated at conspecific female breeding gallery entrances before being admitted or allowed to mate. Some "silent" males entered and/or mated, and some stridulating males did neither, but these were not common. Timing data were not obtained for all pairs. After locating the entrance, L. oregonus usually (22 of 24) stridulated by 0-6 min and were admitted by 0-17 min, without copulating first. In 50 L. californicus pairs, 25 mated at gallery entrances, 7 males attempted to mate and 18 did not make any attempts. In pairs which mated, males usually (24 of 25) stridulated by 0-13 min, were in mating position by 1-46 min ($\bar{x}=16.41$, $n=23$), copulated for 3.75-9.5 min ($\bar{x}=6.94$, $n=23$), and usually resumed stridulation and/or attempted to enter the gallery after disengagement. Males which attempted to mate all stridulated, by 1-6 min. The remaining L. californicus usually (14 of 18) stridulated by 0-7 min and entered by 0-28. Some males in each group took longer to stridulate or enter. Several L. californicus and a few L. oregonus males scratched the female elytra rhythmically with their mandibles. Rivalry behavior of males at attractive female galleries was difficult to elicit. Two

prolonged fights and several brief conflicts were observed for L. californicus, and L. oregonus rivals gradually dislodged resident males in two cases. Field behavior contained the same elements as laboratory behavior.

Male stridulation occurred in two basic patterns. In stress and "rivalry" (not associated with vigorous fighting) situations, males produced continuous runs of short, single, ungrouped chirps. One direction of abdominal motion was acoustically effective, and (on our equipment) toothstrikes usually "pointed" downward in oscillograms. In premating and postmating situations, males produced intermittent series of longer, alternating major and minor chirps. Both directions of abdominal motion were acoustically effective. Major chirp toothstrikes "pointed" downward, whereas minor chirp toothstrikes "pointed" upward. In most males, major chirps had similar numbers of toothstrikes, shorter durations and faster toothstrike rates than minor chirps. L. oregonus had faster stress and premating chirp rates than L. californicus, shorter series durations, shorter minor chirp durations, and fewer toothstrikes in both major and minor chirps. Toothstrike rates varied considerably among males but did not differentiate between species. There were some differences between 1975 and 1976 samples within species. L. californicus had slightly but significantly faster chirp rates and shorter series after mating than before. Atypical chirps were noted in several males. All chirps were "simple," i.e. not interrupted. No female stridulation was detected.

The most important questions remaining involve identification of aggregation pheromones, studies of chemoacoustic behavior and inter-specific response, and establishment of chirp stimulus and function.

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APPENDICES

APPENDIX I
LIST OF SPECIES IN THE
GENUS LEPERISINUS REITTER

For convenience, references have been placed in the BIBLIOGRAPHY.

- aculeatus (Say) - Described in Hylesinus by Say (1824), placed in Leperisinus by Swaine (1918); U. S. and Canada. Synonyms are: (1) L. cinereus, described by Swaine (1917), declared synonymous by S. L. Wood (1957); (2) L. imperialis, described in Hylesinus by Eichhoff (1868), considered synonymous by Underhill (1951, unpublished thesis), declared synonymous by S. L. Wood (1977, in press).
- bicolor Eggers - Described by Eggers (1939); Burma.
- bimaculatus Schedl - Described by Schedl (1936); Australia.
- californicus Swaine - Described by Swaine (1916); U. S. and Canada. Synonym is L. hoferi, described by Blackman (1943), declared synonymous by S. L. Wood (1971).
- criddlei Swaine - Described by Swaine (1918); U. S. and Canada.
- fasciatus (LeConte) - Described in Hylesinus by LeConte (1868), placed in Leperisinus by Swaine (1918); U. S. and Canada.
- fraxini (Panzer) - Described in Hylesinus by Panzer (1799), placed in Leperisinus by Reitter (1913); Europe, North Africa, Russia.
- fraxinoides Schedl - Described by Schedl (1959); India.
- guatemalensis Wood - Described by S. L. Wood (1967); Guatemala.
- mexicanus Wood - Described by S. L. Wood (1956); Mexico.
- oregonus Blackman - Described by Blackman (1943); U. S.
- orni (Fuchs) - Described in Hylesinus by Fuchs (1906), placed in Leperisinus by Reitter (1913), validity supported by Strand (1963) and Allen (1969); Europe.
- pruinus (Eichhoff) - Described in Hylesinus by Eichhoff (1868), placed in Leperisinus by Swaine (1913); U. S.
- regius Schedl - Described by Schedl (1942); New Guinea.
- tricolor Schedl - Described by Schedl (1938); Australia.
- tupolevi (Stark) - Described in Hylesinus by Stark (1936); Russia. Some retain it in Hylesinus (Pfeffer, 1944), and others place it in Leperisinus (Eggers, 1942; Schedl, letter, Jan. 25, 1978).
- wachtli (Reitter) - Described in Hylesinus by Reitter (1887), placed in Leperisinus by Reitter (1913); Europe.

Five species described initially (Schedl, 1942 and 1943a) in "Lep-ericinus" (printer's error for Lepicerinus) were erroneously recorded in the Zoological Record (Vol. 82 and 83) as species of Leperisinus but are correctly placed in Cryphalomorphus Schaufuss, of which Lepicerinus is a junior synonym, according to Schedl (letter, Jan. 25, 1978).

S. L. Wood (letter, Jan. 16, 1978) may place Leperisinus Reitter in synonymy under the Old World genus Hylesinus Fabricius. Leperisinus would be the only species group within Hylesinus represented in North or South America (S. L. Wood, letter, Jan. 31, 1978). I have chosen to use the name "Leperisinus," since the synonymy has not yet been published, and because most North American literature of the past 60 years uses "Leperisinus."

APPENDIX II
INDIVIDUAL LISTINGS OF METHODS
USED FOR AUDIORECORDING AND
BEHAVIORAL OBSERVATION

TABLE XXVI. PREPARATIONS FOR AUDIORECORDING MALE LEPERISINUS SPP. AT FEMALE BREEDING GALLERY ENTRANCES

Pair no.	Date of recording	Days since female was introduced	Days since female was collected*	Days since male was collected*	Size of bit, if hole was drilled; and method of confinement of female
<u>L. californicus</u>					
CF20	6/13/75	5	18	16	plastic tubing mini-cage
CF21	6/14/75	6	19	17-19	plastic tubing mini-cage
CF22	6/17/75	9	21	20-22	plastic tubing mini-cage
CF23	6/11/75	3	15	14-16	plastic tubing mini-cage
CF24	5/09/75	18 or less	30-42	30-42	release into cage w/log
CF25	5/05/75	14 or less	26-38	26-38	release into cage w/log
CL01	6/01/76	2.	5.5	5.5	7/64 inch; screen
CL02	6/01/76	about 8***	23.	6.	7/64 inch?; screen
CL03	6/01/76	2.75	6.	6.	7/64 inch; screen
CL04	6/01/76	2.75	6.	6.	7/64 inch; screen
CL05	6/01/76	2.75	6.	6.	7/64 inch; screen
CL06	6/01/76	0.75	6.5	6.5	5/64 inch; screen
CL07	6/02/76	1.75	7.	7.	5/64 inch; screen
CL08	6/02/76	unknown****	7?	7.	self-introduced****
CL09	6/02/76	1.75	7.	7.	5/64 inch; screen
CL10	6/02/76	1.75	7.5	7.5	5/64 inch; screen
CL11	6/03/76	2.	7.5	7.5	5/64 inch; screen
CL12	6/03/76	2.	7.5	7.5	5/64 inch; screen
<u>L. oregonus</u>					
OR09	6/10/75	2	13	13-15	plastic tubing mini-cage
OR10	6/10/75	3	13	13-15	plastic tubing mini-cage
OR11	6/13/75	5	16	16-18	plastic tubing mini-cage
OR12	6/24/75	6	27-29	27-29	gelatin capsule half
OR13	6/27/75	9	30-32	30-32	gelatin capsule half
ORnn**	6/30/75	3	33-35	33-35	gelatin capsule half
OR14	6/30/75	12	33-35	33-35	plastic tubing mini-cage
OR15	6/30/75	—	—	33-35	abandoned female gallery
RG01	6/17/76	2.25	2.5	2.5	5/64 inch?; screen
RG02	6/17/76	2.25	2.5	2.5	5/64 inch?; screen
RG03	6/17/76	2.25	2.5	2.5	5/64 inch?; screen
RG04	6/17/76	2.5	2.5	2.5	5/64 inch?; screen
RG05	6/17/76	2.5	2.5	2.5	5/64 inch?; screen
RG06**	6/17/76	2.5	2.5	2.5	5/64 inch?; screen
RG07**	6/18/76	2.5	2.75	2.75	5/64 inch?; screen
RG08					
to	6/18/76	2.5	2.75	2.75	5/64 inch?; screen
RG13					

* Laboratory-fed (CF24-25); picked off fallen tree (CF20-23, OR09-15); trapped at caged, infested logs (CL01-12); excised from overwintering burrows (RG01-13).

** Not enough chirps were recorded for acoustic analysis.

*** Female was in cooler for 13 of 21 days after introduction.

**** Female probably escaped from a drilled hole introduction.

TABLE XXVII. PREPARATIONS FOR PAIRING BEHAVIOR STUDIES ON 1976 LEPERI-SINUS CALIFORNICUS WHICH WERE NOT AUDIORECORDED, OR RECORDED BUT NOT ANALYZED

Pair no.	Date	Use of acoustic equipment	Days since female was introduced *	Days since both sexes were collected**	Size of bit, if hole was drilled; and method of confinement of female
1	5/28	no	1.5	2.	7/64 inch; screen
2	5/28	no	1.5	2.	7/64 inch; screen
3	5/31	no	1.5	5.	7/64 inch; screen
4	5/31	no	1.5	5.	7/64 inch; screen
5	5/31	no	1.5	5.	7/64 inch; screen
6	5/31	no	1.5	5.	7/64 inch; screen
7	5/31	no	1.5	5.	7/64 inch; screen
8	5/31	no	1.75	5.	7/64 inch; screen
9	5/31	no	1.75	5.	7/64 inch; screen
10	5/31	no	1.75	5.	7/64 inch; screen
11	5/31	no	3.	5.	razor cut; screen***
12	5/31	no	3.	5.	razor cut; screen***
13	5/31	yes****	1.75	5.	7/64 inch; screen
14	5/31	yes****	2.	5.5	7/64 inch; screen
15	6/01	yes*****	2.	5.5	7/64 inch; screen
16	6/01	yes	2.	5.5	7/64 inch; screen
17	6/01	yes	2.75	6.	7/64 inch; screen
18	6/02	yes	1.75	7.	5/64 inch; screen
19	6/03	yes	2.	7.5	5/64 inch; screen
20	6/03	yes	2.25	8.	5/64 inch; screen
21	6/03	yes	2.25	8.	5/64 inch; screen
22	6/09	no	7.	13.5	5/64 inch; gelatin capsule half
23	6/09	no	7.	13.5	5/64 inch; gelatin capsule half
24	6/09	no	7.	14.	5/64 inch; gelatin capsule half
25	6/09	no*****	7.	14.	5/64 inch; gelatin capsule half
26	6/09	no	7.	14.	5/64 inch; gelatin capsule half
27	6/09	no	7.	14.	5/64 inch; gelatin capsule half
28	6/09	no	7.	14.	5/64 inch; gelatin capsule half
29	6/09	no	7.	14.	5/64 inch; gelatin capsule half
30	6/09	no	7.25	14.	5/64 inch; gelatin capsule half
31	6/09	no	7.25	14.	5/64 inch; gelatin capsule half
32	6/09	no	7.25	14.	5/64 inch; gelatin capsule half
33	6/09	no	7.25	14.	5/64 inch; gelatin capsule half
34	6/09	no	7.25	14.	5/64 inch; gelatin capsule half

*to nearest quarter-day

**to nearest half-day; trapped at caged, infested logs

***re-introduced after first (drilled hole) introduction failed

****recorded, but chirps too soft and mostly buried in baseline

*****same female as for male CL01, which was recorded

*****same male as in pair 24, but matings were 36 min apart and behavioral sequences seemingly complete enough to be counted as two separate observations

TABLE XXVIII. METHODS FOR STRESS AND "RIVALRY" AUDIORECORDINGS OF LEPERISINUS SPP.

Male	Date of recording	Days since male was collected	Circumstances under which male was stimulated to stridulate
<u>L. californicus stress:</u>			
CF16	6/11/75	14-16	hand held - was pulled away from a female gallery (because an external noise was preventing audiorecording), tried to return to the female and ran all over the microphone, but was recaptured
CF17	6/14/75	17-19	hand held
CF18	6/14/75	17-19	was being pinched by the microphone and also had a broken leg
CF19	6/14/75	17-19	hand held - had walked away from a female gallery entrance (while the microphone was being adjusted) but was recaptured - while at the gallery, had been in mating position for 4 min
CLO5	6/01/76	6	hand held - had walked away from a female gallery, without apparent external disturbance, but was recaptured - had mated while at the gallery
CL13	6/01/76	6	hand held - had been (accidentally) scared away from a female gallery entrance
<u>L. oregonus stress:</u>			
ORO1	6/10/75	13-15	hand held
ORO2	6/10/75	13-15	hand held
ORO3	6/10/75	13-15	hand held
ORO4	6/10/75	13-15	hand held
ORO5	6/13/75	16-18	hand held - had been (accidentally) hit with the microphone while at a female gallery entrance, walked away, stress-chirping, but was recaptured
<u>L. californicus "rivalry":*</u>			
CL14	6/01/76	6	two males at a female gallery entrance - the resident (which was dislodged) seemed to be chirping - the rival was recorded soon afterwards at this gallery (male CLO2)
<u>L. oregonus "rivalry":*</u>			
ORO6	6/19/75	22-24	two males placed head-first, one behind the other in a drilled hole under a screen
ORO7	6/20/75	23-25	two males placed facing each other in an enlarged crevice under a screen
ORO8	6/27/75	30-32	two males at a female gallery entrance - the resident (which was dislodged) seemed to be chirping - the rival was recorded soon afterwards at this gallery (male OR13)

* see sections on rivalry behavior for details

APPENDIX III
INDIVIDUAL LISTINGS OF
DESCRIPTIVE STATISTICS FOR CHIRPS AND SERIES
AND RESULTS OF TESTS WITHIN MALES

Legend for Tables XXIX-XXXVIII: C.V., coefficient of variation (percent); cont., contest; crnh., "crunchy"-sounding chirps; G, grouping within a male at .01 probability level, using Mann-Whitney U-test for two groups and Simultaneous Test Procedure (with U-statistic) for more than two groups; prem., premating; post., postmating; S.E., standard error of the mean; skip., chirps in series where alternate chirps were "skipped"; soft., soft single chirps.

For chirps: number of toothstrikes per sec = $1000(\text{number of toothstrikes per chirp} / \text{chirp duration in msec})$; regression y = number of toothstrikes per chirp; regression x = chirp duration in msec.

For series: number of chirps per sec = $1000(\text{number of chirps per series} / \text{series duration in msec})$; regression y = number of chirps per series; regression x = series duration in msec.

- * means regression significant at .05 probability level
- ** means regression significant at .01 probability level
- *** means regression significant at .0005 probability level

TABLE XXIX. STRESS AND "RIVALRY" CHIRPS OF L. CALIFORNICUS MALES

Male Situ-	Chirp	No. of toothstrikes				Duration (msec)			
		Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
CF16 stress	single	46.4	19-67	4.16	34.7	16.2	5.75-24.0	1.46	35.0
CF17 stress	single	17.1	6-28	1.96	44.4	10.8	5.25-19.5	1.07	38.1
CF18 stress	single	10.7	5-17	1.11	39.9	8.4	2.5-15.5	1.07	48.9
CF19 stress	single	10.6	4-16	0.97	35.3	8.7	4.0-12.25	0.76	33.8
CLO5 stress	single	20.9	8-32	1.71	31.7	13.7	7.0-25.5	1.35	38.0
CL13 stress	single	37.5	11-62	3.33	34.4	24.2	5.5-44.0	2.55	40.9
CL14 rivalry	single	29.5	8-58	3.64	32.7	17.2	6.75-26.0	1.35	30.3

n=15 is sample size

TABLE XXIX. (Continued)

Male Situation	Chirp type	No. of toothstrikes per sec				Regression results	
		Mean	Range	S.E.	C.V.	Slope	R-squared
CF16 stress	single	2887.	2554.-3304.	62.0	8.3	2.75***	.937
CF17 stress	single	1545.	1000.-1931.	68.5	17.2	1.67***	.825
CF18 stress	single	1439.	640.-2333.	126.9	34.2	0.76**	.533
CF19 stress	single	1255.	762.-1818.	86.0	26.5	0.90**	.504
CLO5 stress	single	1562.	1059.-2118.	71.7	17.8	1.09***	.733
CL13 stress	single	1605.	1292.-2000.	48.8	11.8	1.27***	.942
CL14 rivalry	single	1676.	962.-2600.	145.7	33.7	1.87**	.478

n=15 is sample size

TABLE XXIX. (Continued)

Male Situation	Chirp type	No. of chirps per sec			
		Mean	Range	S.E.	C.V.
CF16 stress	single	5.10	1.5-6.5	.427	26.5
CF17 stress	single	3.20	1.0-4.5	.318	31.4
CF18 stress	single	2.25	0.5-4.5	.403	56.7
CF19 stress	single	5.75	2.5-7.5	.574	31.6
CLO5 stress	single	4.80	4.5-5.0	.082	5.4
CL13 stress	single	3.75	3.0-5.0	.214	18.1
CL14 rivalry	single	3.25	1.5-4.0	.227	22.1

n=10 is sample size

TABLE XXX. STRESS AND "RIVALRY" CHIRPS OF L. OREGONUS MALES

Male	Situ- ation	Chirp type	No. of toothstrikes				Duration (msec)			
			Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
ORO1	stress	single	9.5	7-15	0.58	23.9	7.5	4.75-13.0	0.57	29.3
ORO2	stress	single	13.9	6-21	1.11	31.0	11.1	5.25-14.0	0.60	20.7
ORO3	stress	single	18.3	12-22	0.71	15.0	16.0	11.25-22.25	0.78	19.0
ORO4	stress	single	13.4	8-27	1.42	41.0	7.0	3.0-14.25	0.81	45.0
ORO5	stress	single	7.9	6-12	0.47	23.1	6.4	4.25-11.0	0.47	28.2
ORO6	rivalry	single	10.7	5-15	0.79	28.5	9.2	3.75-13.75	0.75	31.9
ORO7	rivalry	single	16.6	9-22	1.03	24.0	15.0	6.5-22.25	1.16	29.9
ORO8	rivalry	single	15.1	9-20	0.78	20.0	16.3	8.0-20.25	0.88	20.9

n=15 is sample size

TABLE XXX. (Continued)

Male	Situ- ation	Chirp type	No. of toothstrikes per sec				Regression results	
			Mean	Range	S.E.	C.V.	Slope	R-squared
ORO1	stress	single	1280.	1053.-1474.	28.9	8.7	0.99***	.932
ORO2	stress	single	1239.	851.-1585.	58.6	18.3	1.50***	.646
ORO3	stress	single	1161.	764.-1429.	49.1	16.4	0.40	.199
ORO4	stress	single	2005.	1391.-3000.	105.2	20.3	1.63***	.859
ORO5	stress	single	1248.	1091.-1412.	26.7	8.3	0.97***	.926
ORO6	rivalry	single	1192.	1000.-1412.	33.3	10.8	0.98***	.873
ORO7	rivalry	single	1163.	557.-1702.	74.3	24.7	0.47*	.280
ORO8	rivalry	single	939.	839.-1125.	20.1	8.3	0.84***	.893

n=15 is sample size

TABLE XXX. (Continued)

Male	Situ- ation	Chirp type	No. of chirps per sec			
			Mean	Range	S.E.	C.V.
ORO1	stress	single	9.60	7.0-11.5	.562	18.5
ORO2	stress	single	8.15	2.5-11.0	.992	38.5
ORO3	stress	single	4.35	1.5- 7.0	.592	43.0
ORO4	stress	single	(insufficient chirps)			
ORO5	stress	single	6.45	6.0- 7.5	.138	6.8
ORO6	rivalry	single	4.90	4.0- 6.0	.194	12.5
ORO7	rivalry	single	3.20	1.5- 4.5	.367	36.2
ORO8	rivalry	single	3.95	2.5- 4.5	.229	18.3

n=10 is sample size

TABLE XXXI. CHIRPS OF 1975 L. CALIFORNICUS MALES DURING PAIRING

Male	Situ- ation type	Chirp type	No. of toothstrikes				Duration (msec)					
			Mean	G	Range	S.E.	C.V.	Mean	G	Range	S.E.	C.V.
CF20	prem.	major	80.3	a	23-112	7.04	33.9	40.7	a	18.0-56.0	3.32	31.5
	prem.	minor	86.1	a	42-125	6.89	31.0	75.1	b	26.0-94.5	5.26	27.1
	post.	major	73.5	a	48-108	5.47	28.8	33.8	a	19.3-54.0	3.02	34.7
	post.	minor	79.5	a	48-114	5.69	27.7	63.5	b	40.5-88.5	3.44	20.9
CF21	prem.	major	87.1	a	45-118	5.93	26.3	38.5	a	25.3-54.0	2.42	24.3
	prem.	minor	86.8	a	36-105	4.84	21.6	64.5	b	36.5-80.0	3.15	18.9
CF22	prem.	major	83.5	a	52-105	3.67	17.0	46.6	a	29.5-56.5	1.67	13.8
	prem.	minor	77.6	a	35-102	5.26	26.2	55.7	a	19.5-88.0	4.58	31.9
CF23	prem.	major	74.2	b	57- 89	2.82	14.7	39.0	b	30.3-47.5	1.23	12.3
	prem.	minor	54.3	a	13- 73	4.26	30.4	29.3	a	11.0-42.5	1.94	25.6
CF24	prem.	major	90.0	b	40-106	4.68	20.1	48.9	b	24.5-58.0	2.20	17.5
	prem.	minor	87.3	b	67-107	3.20	14.2	64.9	c	38.5-86.5	3.64	21.7
	later	wierd	18.9	a	6- 39	2.47	50.5	13.2	a	4.0-24.8	1.64	48.3
CF25	prem.	major	49.8	a	32- 64	2.62	20.4	29.5	a	18.5-40.0	1.84	24.2
	prem.	minor	51.6	a	24- 71	3.37	25.3	72.7	b	47.0-96.0	3.38	18.0
n=15 is sample size per male-situation-chirp type												

n=15 is sample size per male-situation-chirp type

TABLE XXXI. (Continued)

Male	Situ- ation type	Chirp type	No. of toothstrikes per sec				Regression results		
			Mean	G	Range	S.E.	C.V.	Slope	R-squared
CF20	prem.	major	1953.	b	1278.-2423.	75.8	15.0	1.97***	.864
	prem.	minor	1164.	a	845.-1615.	58.1	19.4	1.07***	.671
	post.	major	2221.	b	1882.-2602.	54.4	9.5	1.78***	.964
	post.	minor	1244.	a	850.-1562.	48.7	15.2	1.38***	.694
CF21	prem.	major	2285.	b	1324.-2917.	114.8	19.5	1.81**	.543
	prem.	minor	1348.	a	986.-1642.	52.9	15.2	1.16**	.575
CF22	prem.	major	1797.	b	1320.-2171.	62.3	13.4	1.42**	.413
	prem.	minor	1434.	a	1023.-1798.	58.2	15.7	1.01***	.782
CF23	prem.	major	1903.	a	1617.-2137.	38.5	7.8	1.96***	.732
	prem.	minor	1820.	a	1182.-2149.	68.9	14.7	2.04***	.863
CF24	prem.	major	1832.	b	1488.-2019.	37.4	7.9	2.00***	.888
	prem.	minor	1377.	a	1130.-1740.	52.1	14.7	0.69**	.610
		later wierd	1471.	ab	768.-2250.	105.2	27.7	1.17**	.603
CF25	prem.	major	1713.	b	1422.-2162.	43.8	9.9	1.34***	.876
	prem.	minor	711.	a	400.- 906.	37.5	20.4	0.63*	.396

n=15 is sample size per male-situation-chirp type

CF20 is the same male as CF16.

TABLE XXXII. CHIRPS OF 1976 L. CALIFORNICUS MALES DURING PAIRING

Male	Situation	Chirp type	Number of toothstrikes					Duration (msec)				
			Mean	G	Range	S.E.	C.V.	Mean	G	Range	S.E.	C.V.
CLO1	cont.	major	78.4	a	51-105	4.16	20.6	49.3	a	33.0-63.5	2.70	21.2
	cont.	minor	81.7	a	51-105	3.94	18.7	65.9	b	36.0-81.5	3.16	18.6
CLO2	cont.	major	69.0	a	51-85	2.81	15.8	31.7	a	22.5-41.5	1.56	19.1
	cont.	minor	64.7	a	37-94	4.37	26.1	80.7	b	49.0-113.0	4.25	20.4
	prem.	major	63.9	a	45-86	2.83	17.2	27.2	a	20.5-37.0	1.27	18.1
	prem.	minor	62.5	a	47-84	3.18	19.7	59.1	b	40.5-81.5	3.42	22.4
	post.	major	62.0	a	44-76	2.58	16.1	27.8	a	20.0-34.5	1.00	14.0
	post.	minor	58.9	a	41-77	3.01	19.8	61.9	b	42.5-83.5	3.01	18.8
CLO3	prem.	major	86.1	b	46-119	6.10	27.4	53.8	b	19.8-90.5	5.24	37.7
	prem.	minor	87.5	b	57-111	4.43	19.6	81.5	c	52.5-99.0	3.75	17.8
	prem.	crnh.	24.1	a	7-54	3.19	51.3	53.4	b	15.0-125.0	6.36	46.1
	post.	soft.	18.5	a	7-33	2.02	42.1	21.2	a	6.5-33.0	1.94	35.4
	post.	major	85.4	b	75-98	1.78	8.1	66.4	bc	47.0-81.0	2.44	14.2
	post.	minor	78.8	b	69-91	1.89	9.3	66.3	bc	49.0-95.0	3.33	19.4
CLO4	prem.	major	108.7	b	93-122	2.24	8.0	48.4	b	38.0-60.0	1.65	13.2
	prem.	minor	101.1	b	80-119	2.57	9.8	86.2	c	70.5-103.5	2.70	12.1
	prem.	cluck	14.1	a	7-25	1.46	40.3	7.6	a	5.5-10.5	0.49	24.7
CLO5	prem.	major	66.8	a	55-88	2.09	12.1	50.4	a	34.0-66.0	2.45	18.8
	prem.	minor	65.6	a	52-88	2.91	17.2	83.6	b	65.0-110.0	3.22	14.9
CLO6	prem.	major	73.3	a	50-95	2.99	15.8	62.1	a	46.5-80.0	2.12	13.2
	prem.	minor	72.2	a	43-105	3.87	20.8	84.9	b	63.5-109.5	3.49	15.9
	post.	major	85.9	a	73-100	2.15	9.7	61.4	a	49.0-79.5	2.00	12.6
	post.	minor	83.2	a	58-101	3.69	17.2	76.3	b	61.5-90.5	2.43	12.3
CLO7	prem.	major	73.5	a	64-87	1.62	8.6	46.5	a	36.5-73.0	2.75	23.0
	prem.	minor	64.9	a	34-90	4.26	25.4	66.1	ab	40.5-98.0	4.92	28.8
	post.	major	65.9	a	26-92	4.76	28.0	43.7	a	26.5-67.0	3.47	30.7
	post.	minor	58.1	a	30-86	4.32	28.8	67.4	b	50.0-98.5	3.17	18.2
CLO8	prem.	major	83.8	a	71-92	1.51	7.0	53.2	a	40.0-66.0	1.94	14.1
	prem.	minor	81.5	a	47-101	3.61	17.1	73.9	b	41.5-92.5	3.87	20.3
CLO9	prem.	major	55.6	a	38-69	2.25	15.7	48.0	a	27.5-65.5	3.08	24.9
	prem.	minor	50.5	a	36-62	2.18	16.7	89.0	b	73.0-122.5	3.52	15.3
CL10	prem.	major	90.2	a	32-110	5.12	22.0	49.1	a	33.5-62.0	2.07	16.4
	prem.	minor	86.5	a	45-118	4.93	22.1	68.6	b	48.0-80.5	2.75	15.5
CL11	prem.	major	92.3		57-116	3.65	15.3	48.7		36.5-66.5	2.13	16.9
	post.	major	82.3		68-105	2.96	14.0	49.1		41.0-58.0	1.39	11.0
CL12	post.	major	100.3	a	72-115	3.18	12.3	66.0	a	49.0-87.5	2.66	15.6
	post.	minor	93.3	a	58-125	5.21	21.6	71.3	a	42.0-94.5	3.48	18.9

n=15 is sample size per male-situation-chirp type

When CLO7's premating chirps are tested alone, without postmating, using the Mann-Whitney U-test, major chirp duration is less than minor chirp duration.

CL11's minor chirps were too soft and buried in the baseline to be analyzed.

(Continued)

TABLE XXXII. (Continued)

Male	Situ- ation type	Chirp	Number of toothstrikes per sec				Regression results		
			Mean	G	Range	S.E.	C.V.	Slope	R-squared
CLO1	cont. major		1605.	b	1291.-1879.	52.3	12.6	1.24***	.648
	cont. minor		1247.	a	994.-1417.	31.3	9.7	1.07***	.744
CLO2	cont. major		2194.	c	1976.-2407.	37.5	6.6	1.69***	.887
	cont. minor		798.	a	637.- 975.	27.9	13.5	0.89***	.746
	prem. major		2358.	c	2069.-2607.	45.4	7.5	2.01***	.822
	prem. minor		1072.	b	720.-1281.	35.7	12.9	0.74***	.633
	post. major		2231.	c	1831.-2421.	40.0	6.9	2.31***	.804
	post. minor		954.	ab	785.-1148.	23.4	9.5	0.87***	.760
CLO3	prem. major		1692.	e	1315.-2426.	84.1	19.6	1.11***	.904
	prem. minor		1072.	bc	919.-1285.	22.9	8.3	1.08***	.832
	prem. crnh.		448.	a	287.- 713.	27.5	23.7	0.44***	.785
	post. soft.		891.	b	370.-1257.	62.4	27.1	0.76**	.536
	post. major		1307.	d	1103.-1830.	48.8	14.5	0.34	.218
	post. minor		1214.	cd	958.-1426.	40.3	12.9	0.45***	.628
CLO4	prem. major		2267.	b	1933.-2675.	53.2	9.1	1.04**	.586
	prem. minor		1182.	a	899.-1342.	31.3	10.3	0.52*	.294
	prem. cluck		1845.	b	1077.-2609.	138.0	29.0	2.03**	.454
CLO5	prem. major		1364.	b	965.-1735.	69.9	19.9	0.26	.094
	prem. minor		786.	a	645.- 892.	19.7	9.7	0.74***	.663
CLO6	prem. major		1184.	b	952.-1484.	39.7	13.0	0.84*	.353
	prem. minor		862.	a	558.-1106.	45.6	20.5	0.40	.132
	post. major		1413.	c	1119.-1676.	42.9	11.8	0.47	.196
	post. minor		1089.	b	868.-1318.	35.4	12.6	1.08**	.503
CLO7	prem. major		1626.	b	1068.-1924.	55.9	13.3	0.43**	.535
	prem. minor		999.	a	739.-1258.	37.5	14.6	0.76***	.769
	post. major		1523.	b	981.-2125.	62.5	15.9	1.25***	.833
	post. minor		858.	a	589.-1170.	47.5	21.5	0.84*	.383
CLO8	prem. major		1592.	b	1288.-1775.	38.7	9.4	0.55**	.511
	prem. minor		1116.	a	958.-1317.	30.5	10.6	0.81***	.762
CLO9	prem. major		1197.	b	927.-1527.	52.1	16.9	0.56**	.582
	prem. minor		576.	a	404.- 782.	29.6	19.9	0.15	.057
CL10	prem. major		1836.	b	955.-2371.	90.0	19.0	1.74**	.498
	prem. minor		1256.	a	938.-1584.	47.7	14.7	1.40**	.614
CL11	prem. major		1904.		1476.-2208.	50.3	10.2	1.34**	.613
	post. major		1678.		1394.-1934.	45.6	10.5	1.40**	.434
CL12	post. major		1538.	b	1210.-1918.	52.7	13.3	0.70*	.346
	post. minor		1312.	a	960.-1491.	39.7	11.7	1.27***	.721

n=15 is sample size per male-situation-chirp type

TABLE XXXIII. CHIRPS OF 1975 L. OREGONUS MALES DURING PAIRING

Male	Situation type	No. of toothstrikes				Duration (msec)			
		Mean	G	Range	S.E. C.V.	Mean	G	Range	S.E. C.V.
OR09	prem. major	45.2	a	15-68	4.97 42.6	33.9	a	16.0-48.0	2.68 30.6
	prem. minor	44.7	a	24-64	3.64 31.5	32.7	a	19.0-51.0	2.58 30.6
OR10	prem. major	45.1	a	19-71	3.91 33.6	25.7	a	8.3-51.5	3.20 48.1
	prem. minor	51.8	a	24-76	3.62 27.1	39.5	b	18.0-54.0	2.47 24.2
OR11	prem. major	65.1	a	34-83	3.02 18.0	29.4	a	20.3-38.5	1.47 19.4
	prem. minor	69.7	a	51-87	2.97 16.5	44.0	b	28.5-58.5	2.04 18.0
OR12	prem. major	51.5	a	14-69	4.37 32.8	41.8	a	13.0-57.5	3.25 30.1
	prem. minor	60.8	a	45-71	1.98 12.6	51.8	b	36.5-66.5	2.44 18.2
OR13	prem. major	74.8	a	36-89	3.45 17.9	40.5	a	27.5-45.5	1.18 11.3
	prem. minor	66.3	a	32-87	3.88 22.7	45.6	a	23.5-60.0	2.70 22.9
OR14	prem. major	63.1	b	30-93	4.60 28.2	50.1	b	25.0-63.0	2.62 20.9
	prem. minor	45.6	a	22-67	3.28 27.8	35.8	a	19.0-50.0	2.50 27.1
	prem. skip.	46.9	a	13-62	3.46 27.6	34.7	a	18.5-42.0	1.62 17.5
OR15	odd major	51.3	a	22-62	2.84 21.5	40.0	b	26.5-50.0	1.73 16.7
	odd minor	44.3	a	34-53	1.63 14.3	34.2	a	24.0-40.0	1.18 13.3

n=15 is sample size per male-situation-chirp type, except in one case
n=14 is sample size of OR14-prem.-skip

TABLE XXXIII. (Continued)

Male	Situation type	No. of toothstrikes per sec				Regression results	
		Mean	G	Range	S.E. C.V.	Slope	R-squared
OR09	prem. major	1302.	a	576.-1781.	85.1 25.3	1.62***	.767
	prem. minor	1374.	a	1043.-1647.	42.1 11.9	1.32***	.873
OR10	prem. major	1961.	b	1086.-3520.	176.0 34.8	0.94**	.595
	prem. minor	1310.	a	1075.-1583.	152.6 11.6	1.31***	.796
OR11	prem. major	2295.	b	883.-3210.	143.0 24.1	-0.03	.0002
	prem. minor	1602.	a	1295.-2104.	55.4 13.4	1.05**	.526
OR12	prem. major	1229.	a	958.-1659.	58.5 18.4	1.11***	.678
	prem. minor	1189.	a	992.-1459.	30.0 9.8	0.71***	.778
OR13	prem. major	1834.	b	1309.-2132.	53.6 11.3	2.58***	.777
	prem. minor	1455.	a	1362.-1588.	60.6 4.2	1.42***	.975
OR14	prem. major	1285.	a	556.-2058.	94.9 28.6	0.71	.165
	prem. minor	1284.	a	1000.-1654.	49.6 15.0	1.08***	.678
	prem. skip.	1326.	a	703.-1594.	65.1 18.4	1.88***	.772
OR15	odd major	1279.	a	710.-1500.	48.6 14.7	1.36***	.681
	odd minor	1296.	a	1117.-1417.	20.2 6.0	1.26***	.819

n=15 is sample size per male-situation-chirp type, except in one case
n=14 is sample size of OR14-prem.-skip

TABLE XXXIV. CHIRPS OF 1976 L. OREGONUS MALES DURING PAIRING

Male	Situ- ation	Chirp type	No. of toothstrikes				Duration (msec)					
			Mean	G	Range	S.E.	C.V.	Mean	G	Range	S.E.	C.V.
RG01	prem.	major	34.2	a	18-57	2.61	29.6	20.1	a	12.8-30.0	1.23	23.7
		prem. minor	49.4	b	29-66	2.97	23.3	51.7	b	31.5-70.5	2.70	20.3
RG02	prem.	major	36.6	a	18-58	3.61	38.2	31.7	a	22.0-39.0	1.46	17.8
		prem. minor	39.9	a	16-65	3.78	36.7	41.2	b	29.0-56.0	2.26	21.2
RG03	prem.	major	49.7	a	32-62	2.79	21.7	24.8	a	20.0-30.0	0.87	13.6
		prem. minor	47.4	a	40-56	1.21	9.9	41.4	b	34.5-48.5	1.07	10.0
RG04	prem.	major	46.5	a	16-70	3.91	32.6	30.2	a	13.3-42.5	2.37	30.4
		prem. minor	44.8	a	28-56	2.22	19.2	40.4	b	22.5-57.0	2.46	23.6
RG05	prem.	major	38.5	a	22-56	2.54	25.6	16.1	a	5.8-23.3	1.33	32.1
		prem. minor	37.8	a	10-51	3.56	36.5	33.7	b	11.5-47.0	2.75	31.6
RG08	prem.	major	34.8	a	14-46	2.14	23.8	33.2	a	18.0-43.0	1.85	21.5
		prem. minor	33.2	a	21-43	1.73	20.1	36.5	a	23.0-47.0	1.89	20.0
RG09	prem.	major	28.7	a	12-43	2.24	30.2	21.9	a	11.0-27.5	1.05	18.6
		prem. minor	33.4	a	10-57	3.39	39.3	36.2	b	18.5-45.5	2.16	23.1
RG10	prem.	major	45.8		20-43	4.07	34.4	27.7		8.8-41.0	2.51	35.1
RG11	prem.	major	46.9	a	34-66	2.54	21.0	24.8	a	14.5-33.5	1.42	22.3
		prem. minor	46.3	a	27-63	2.82	23.5	36.5	b	25.0-49.0	1.60	16.9
RG12	prem.	major	24.4	a	6-40	2.38	37.8	20.0	a	6.5-30.5	1.69	32.7
		prem. minor	26.1	a	11-40	2.47	36.7	38.6	b	24.5-51.5	2.18	21.9
RG13	prem.	major	34.8	a	23-68	2.43	38.1	24.9	a	17.5-33.5	1.21	18.8
		prem. major	34.1	a	15-68	3.79	43.0	36.0	b	18.5-51.5	2.77	29.8

n=15 is sample size per male-situation-chirp type

RG10's minor chirps were too soft and buried in the baseline to be analysed

(Continued)

TABLE XXXIV. (Continued)

Male	Situ- ation type	Chirp type	No. of toothstrikes per sec				Regression results		
			Mean	G	Range	S.E.	C.V.	Slope	R-squared
RG01	prem.	major	1732.	b	955.-2510.	112.2	25.1	1.34*	.400
	prem.	minor	956.	a	718.-1181.	30.9	12.5	0.92***	.696
RG02	prem.	major	1129.	a	581.-1611.	74.9	25.7	2.03***	.673
	prem.	minor	956.	a	516.-1287.	65.4	26.5	1.29**	.597
RG03	prem.	major	1996.	b	1542.-2417.	74.2	14.4	2.55***	.630
	prem.	minor	1153.	a	889.-1358.	35.8	12.0	0.20	.032
RG04	prem.	major	1534.	b	1143.-1728.	51.7	13.1	1.50***	.831
	prem.	minor	1131.	a	895.-1377.	43.5	14.9	0.68**	.559
RG05	prem.	major	2551.	b	1487.-4870.	199.3	30.3	1.44**	.570
	prem.	minor	1098.	a	870.-1380.	37.6	13.3	1.22***	.893
RG08	prem.	major	1054.	b	778.-1644.	54.9	20.2	0.87**	.567
	prem.	minor	914.	a	773.-1049.	22.4	9.5	0.83***	.819
RG09	prem.	major	1324.	b	600.-1955.	90.2	26.4	1.09	.264
	prem.	minor	909.	a	444.-1310.	64.0	27.3	1.22**	.603
RG10	prem.	major	1718.		1075.-2442.	100.4	22.6	1.33***	.678
RG11	prem.	major	1912.	b	1667.-2345.	53.3	10.8	1.61***	.815
	prem.	minor	1263.	a	915.-1556.	46.7	14.3	1.44***	.668
RG12	prem.	major	1219.	b	667.-1769.	80.2	25.5	1.14***	.661
	prem.	minor	672.	a	393.-1081.	54.7	31.5	0.74**	.431
RG13	prem.	major	1387.	b	923.-2126.	96.0	26.8	1.82*	.410
	prem.	minor	932.	a	677.-1320.	51.8	21.5	1.17***	.738

n=15 is sample size per male-situation-chirp type

TABLE XXXV. SERIES OF 1975 L. CALIFORNICUS MALES DURING PAIRING

Male Situation	n	Number of chirps				Duration (msec)			
		Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
CF20 premating	9	14.9	7-27	1.79	36.1	1481.	637.5-2738.	187.6	38.0
postmating	10	14.2	9-21	1.10	24.6	1228.	662.5-1925.	112.1	42.3
CF21 premating	10	16.1	6-32	2.28	44.8	1481.	570.0-2950.	209.0	44.6
CF22 premating	10	11.7	6-25	1.68	45.4	1220.	530.0-2650.	183.0	47.4
CF23 premating	10	6.6	4-10	0.88	42.4	768.	350.0-1255.	126.0	51.9
CF24 premating	10	14.9	5-24	1.88	39.8	1286.	365.0-2150.	174.8	43.0

TABLE XXXV. (Continued)

Male Situation	n	No. of chirps per sec				Regression results	
		Mean	Range	S.E.	C.V.	Slope	R-squared
CF20 premating	9	10.1	9.6-11.0	.136	4.0	.0095***	.995
postmating	10	11.7	10.1-13.6	.311	8.4	.0096***	.946
CF21 premating	10	10.8	10.2-11.8	.154	4.5	.0109***	.992
CF22 premating	10	9.7	8.3-11.3	.306	9.9	.0091***	.973
CF23 premating	10	9.2	6.4-11.4	.485	16.7	.0066***	.877
CF24 premating	10	11.8	10.7-13.7	.251	6.7	.0107***	.991

TABLE XXXVI. SERIES OF 1976 L. CALIFORNICUS MALES DURING PAIRING

Male Situation	n	Number of chirps				Duration (msec)			
		Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
CLO1 contest	10	14.6	10-18	0.75	16.2	1546.	1063. -1875.	79.3	16.2
CLO2 contest	6	19.8	10-25	2.18	26.9	2744.	1263. -3550.	331.1	29.6
premating	5	14.0	5-21	3.16	50.5	1633.	512.5-2575.	394.5	54.0
postmating	6	13.2	11-15	0.54	10.1	1483.	1238. -1638.	62.5	10.3
CLO3 premating									
adjusted [*]	10	12.5	8-18	1.25	31.6	1630.	1025. -2338.	159.7	31.0
unadjusted	10	same	same	same	same	1773.	1088. -2763.	190.1	33.9
postmating									
adjusted [*]	10	11.5	6-21	1.44	39.6	1256.	675.0-2350.	164.2	41.3
unadjusted	10	same	same	same	same	1376.	762.5-2700.	198.6	84.3
CLO4 premating	10	15.6	12-25	1.26	25.5	1699.	1313. -2775.	139.1	25.9
CLO5 premating	9	17.6	9-29	1.99	34.0	1936.	1000. -3375.	232.7	36.1
CLO6 premating	10	15.5	11-20	1.07	21.8	1583.	1063. -2163.	113.9	22.8
CLO7 premating									
adjusted ^{**}	10	10.6	5-22	1.71	50.9	1259.	575.0-2650.	214.7	53.9
unadjusted	10	10.1	5-22	1.59	49.7	same	same	same	same
postmating	10	10.0	7-16	0.89	27.9	1066.	687.5-1638.	96.9	28.7
CLO8 premating									
adjusted [*]	10	19.9	11-33	2.07	32.9	2220.	1238. -3750.	233.3	33.2
unadjusted	10	same	same	same	same	2295.	1300. -3750.	222.4	30.1
CLO9 premating									
adjusted [*]	10	10.0	7-16	1.01	32.0	1424.	987.5-2200.	140.8	31.3
unadjusted	10	same	same	same	same	1625.	987.5-2450.	174.2	33.9
CL10 premating									
adjusted [*]	10	28.0	14-42	2.72	30.8	2410.	1163. -3763.	253.3	33.2
unadjusted	10	same	same	same	same	2444.	1163. -3763.	265.4	34.3
CL11 premating	10	15.2	11-22	0.98	20.3	1533.	1113. -2188.	94.7	19.5
postmating	10	13.3	8-20	1.15	27.2	1224.	737.5-1825.	106.2	27.4
CL12 postmating									
adjusted [*]	10	12.8	6-19	1.47	36.2	1604.	700.0-2500.	203.2	40.1
unadjusted	10	same	same	same	same	1915.	700.0-3013.	254.8	42.1

^{*} adjusted for hesitations of 125.-375. msec between chirps in the same series

^{**} adjusted for skipped or very soft minor chirps

Adjustments were for:

CLO3 premating - 11 hesitations in 6 series (1,1,1,2,3,3 per series)

CLO3 postmating - 8 hesitations in 6 series (1,1,1,1,2,2 per series)

CLO7 premating - 5 skips in 2 series (2,3 per series)

CLO8 premating - 7 hesitations in 5 series (1,1,1,2,2 per series)

CLO9 premating - 11 hesitations in 6 series (1,1,2,2,2,3 per series)

CL10 premating - 2 hesitations in 1 series

CL12 postmating - 22 hesitations in 9 series (1,1,1,2,2,3,3,4,5 per series)

(Continued)

TABLE XXXVI. (Continued)

Male Situation	n	No. of chirps per sec				Regression results	
		Mean	Range	S.E.	C.V.	Slope	R-squared
CLO1 contest	10	9.5	8.1-10.9	.263	8.8	.0079**	.709
CLO2 contest	6	7.3	7.0- 7.9	.146	14.7	insufficient data	
premating	5	8.8	8.2- 9.8	.266	6.7	insufficient data	
postmating	6	8.9	8.1- 9.5	.205	5.7	insufficient data	
CLO3 premating							
adjusted	10	7.7	7.2- 8.1	.084	3.5	.0078***	.987
unadjusted	10	7.1	6.5- 7.8	.150	6.7	.0064***	.961
postmating							
adjusted	10	9.2	8.8- 9.7	.103	3.5	.0087***	.995
unadjusted	10	8.6	7.3- 9.7	.271	3.9	.0072***	.973
CLO4 premating	10	9.2	8.7- 9.6	.083	2.8	.0090***	.986
CLO5 premating	9	9.1	8.6- 9.3	.079	2.6	.0085***	.992
CLO6 premating	10	9.8	9.2-10.5	.134	4.3	.0092***	.961
CLO7 premating							
adjusted	10	8.6	7.7- 9.3	.171	6.3	.0079***	.993
unadjusted	10	8.3	6.7- 9.3	.298	11.4	.0072***	.944
postmating	10	9.5	7.5-10.5	.318	10.6	.0086***	.886
CLO8 premating							
adjusted	10	9.0	8.7- 9.8	.104	3.7	.0088***	.986
unadjusted	10	8.6	7.3- 9.8	.222	8.1	.0091***	.957
CLO9 premating							
adjusted	10	7.0	6.0- 8.0	.165	7.4	.0070***	.957
unadjusted	10	6.2	4.7- 7.1	.224	11.4	.0055***	.891
CL10 premating							
adjusted	10	11.7	11.0-12.9	.185	5.0	.0107***	.984
unadjusted	10	11.6	9.9-12.9	.253	6.9	.0100***	.956
CL11 premating	10	9.9	9.5-10.2	.061	1.9	.0103***	.992
postmating	10	10.9	10.1-11.8	.138	4.0	.0107***	.985
CL12 postmating							
adjusted	10	8.1	7.3- 9.0	.163	6.4	.0071***	.978
unadjusted	10	7.0	5.4- 8.6	.325	14.7	.0055***	.913

TABLE XXXVII. SERIES OF 1975 L. OREGONUS MALES DURING PAIRING

Male Situation n	Number of chirps				Duration (msec)			
	Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
OR09 premating 10	9.2	7-10	0.33	11.2	496.0	365.- 600.	21.2	13.5
OR10 premating 10	12.8	10-16	0.61	15.1	723.0	585.- 925.	36.3	15.9
OR11 premating 10	9.5	7-12	0.43	14.3	522.5	375.- 660.	24.5	14.8
OR12 premating 10	8.1	6- 9	0.31	12.3	624.0	395.- 785.	33.8	17.1
OR13 premating 10	11.4	9-14	0.54	15.0	691.0	510.- 835.	34.6	15.8
OR14 premating 10	11.4	4-21	1.45	40.3	730.0	215.-1410.	100.4	43.5
OR15 odd 5	9.2	8-10	0.49	11.9	599.0	505.- 665.	34.7	13.0

TABLE XXXVII. (Continued)

Male Situation n	No. of chirps per sec				Regression results	
	Mean	Range	S.E.	C.V.	Slope	R-squared
OR09 premating 10	18.6	16.7-19.2	.245	4.2	.0145***	.891
OR10 premating 10	17.7	17.0-18.8	.189	18.9	.0165***	.958
OR11 premating 10	18.2	16.2-19.8	.319	5.5	.0163***	.874
OR12 premating 10	13.1	11.5-15.2	.383	9.2	.0080**	.746
OR13 premating 10	16.5	15.7-17.6	.179	8.4	.0153***	.959
OR14 premating 10	15.9	14.7-18.6	.382	7.6	.0144***	.990
OR15 odd 5	15.4	15.0-15.8	.152	2.2	insufficient data	

TABLE XXXVIII. SERIES OF 1976 L. OREGONUS MALES DURING PAIRING

Male Situation	n	Number of chirps				Duration (msec)			
		Mean	Range	S.E.	C.V.	Mean	Range	S.E.	C.V.
RG01 premating	10	9.6	7-13	0.54	17.8	581.0	460.-835.	35.8	19.5
RG02 premating	10	10.2	6-14	0.74	23.0	575.0	305.-770.	47.2	25.9
RG03 premating	10	10.9	9-13	0.38	11.0	557.0	445.-655.	21.4	12.2
RG04 premating	10	9.6	8-11	0.31	10.1	519.5	450.-640.	17.3	10.6
RG05 premating	10	8.6	3-13	0.91	33.4	424.0	145.-615.	45.2	33.7
RG08 premating	8	10.4	3-15	1.39	37.8	546.9	165.-795.	75.5	39.0
RG09 premating	10	10.5	9-12	0.31	9.3	510.5	430.-635.	18.0	11.2
RG10 premating									
adjusted ¹	10	9.4	7-11	0.37	12.5	481.0	335.-585.	24.2	15.9
unadjusted	10	6.8	6- 8	0.25	11.6	same	same	same	same
RG11 premating	10	9.6	7-14	0.65	21.5	456.0	320.-670.	30.6	21.2
RG12 premating	10	10.4	9-11	0.27	8.1	510.5	455.-560.	12.3	7.6
RG13 premating	10	10.9	9-14	0.41	11.8	554.5	520.-700.	16.7	9.5

¹ adjusted for skipped or very soft minor chirps

TABLE XXXVIII. (Continued)

Male Situation	n	No. of chirps per sec				Regression results	
		Mean	Range	S.E.	C.V.	Slope	R-squared
RG01 premating	10	16.6	15.2-18.5	.402	7.7	.0139***	.844
RG02 premating	10	17.9	16.9-20.0	.343	6.0	.0156***	.981
RG03 premating	10	19.6	18.3-20.6	.195	3.1	.0171***	.939
RG04 premating	10	18.5	17.2-19.6	.277	4.7	.0156**	.787
RG05 premating	10	20.4	19.4-21.8	.243	3.8	.0200***	.988
RG08 premating	8	19.0	18.2-21.4	.356	5.3	.0183***	.989
RG09 premating	10	20.6	18.9-21.6	.254	3.9	.0158***	.861
RG10 premating							
adjusted	10	19.7	18.2-21.4	.284	4.6	.0150***	.955
unadjusted	10	14.3	12.0-17.9	.587	13.0	.0069*	.443
RG11 premating	10	21.1	19.3-22.0	.280	4.2	.0210***	.967
RG12 premating	10	20.4	18.0-22.0	.398	6.2	.0149*	.473
RG13 premating	10	19.6	17.1-21.2	.365	5.9	.0216**	.781