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ACOUSTICAL SIGNALS OF PASSALID BEETLES:
COMPLEX REPERTOIRES

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ABSTRACT

Adult passalids produced sounds of 7 basic structural types in at least 13 different behavioral contexts. A given type in a particular behavioral context may be termed a "signal". A total of 31 signals were recorded from 57 species. The presence of the same basic signals in both New World tribes suggests an early origin of the fundamental repertoire. The 14-signal repertoire of *Odontotaenius disjunctus* (Ill.) is larger than previously known for any arthropod and more extensive than those of many vertebrates. The large repertoire is associated with a high level of sociality. *Dendroctonus* beetles, similarly highly social, also have a large repertoire with some signals resembling those of passalids. Convergence in sound signals and social behavior may derive from occupation of similar microhabitats (tree trunks).

RESUMEN

Adultos de Passalidae produjeron sonidos de siete tipos estructurales básicos en por lo menos 13 contextos diferentes de comportamiento. Un tipo dado de sonido en un contexto particular se llama una "señal". De 57 especies se grabaron 31 señales. La presencia de las mismas señales básicas en ambas tribus del Nuevo Mundo sugiere un origen antiguo del repertorio fundamental. El repertorio de *Odontotaenius disjunctus* consta de 14 señales, y es más grande que los previamente conocidos para cualquier artrópodo o aún para muchos vertebrados. El repertorio extensivo está con un alto nivel de socialidad. Los coleópteros *Dendroctonus* también tienen un alto nivel de socialidad asociado con un repertorio acústico muy desarrollado, con ciertas señales parecidas a las de los pasálidos. La convergencia entre señales auditivas y comportamiento social de estos dos grupos puede ser derivada de la ocupación de microhabitats parecidos (troncos de árboles).

Passalids are large (body length 9 to more than 100 mm), primarily tropical beetles that live in tunnels in rotting wood (Schuster 1978). They produce sounds by rubbing 2 spinose areas on the sixth abdominal tergite against the metathoracic wings (Babb 1901, Reyes-Castillo 1970). That sound production is an important aspect of the beetle's behavior and not just incidental is suggested by the presence in some species of wings that are reduced to thin straps enlarged distally. These wings are useless for flight but retain the stridulatory function (Reyes-Castillo 1970). The larvae produce sounds by scraping the reduced metathoracic legs against a file on the mesothoracic coxae (Reyes-Castillo and Jarman 1980).

This paper summarizes the passalid acoustical repertoire and relates this repertoire to what is known concerning sound repertoires of other Coleoptera. Relatively little is known concerning sound repertoires of insects outside the Orthoptera, Homoptera, and Hemiptera. The only other beetle repertoires studied comparatively have been those of Scolytidae (Barr 1969), Hydrophilidae (Ryker 1976), and Cerambycidae (Michelsen 1966). Furthermore, none of the groups mentioned, except perhaps the Scolytidae, has members with the high level of social behavior found in Passalidae (Schuster and Schuster, unpubl.). Study of the acoustical repertoire of passalids, therefore, should be particularly valuable in elaborating the interrelation of communication and social behavior.

MATERIALS AND METHODS

Logs were carefully dissected in the field (Peru, Colombia, Ecuador, Panama, Costa Rica, Guatemala, Belice, Mexico, U.S., Dominican Republic and Puerto Rico, principally) to determine which passalids were found in the same tunnel system. Each such group was caged separately in a terrarium or in a large (15 cm x 2 cm) petri dish. These were kept in my home in places which would maximize the chance of observing relatively rare behavior such as courtship or aggression. One method effectively stimulating such behavior was to introduce other passalids that had been isolated for a week or more into these petri dishes. Sounds could easily be recorded by placing a microphone near the dish. Ambient temperature was measured for each recording. Sounds were recorded on various tape recorders (Schuster 1975a), including a Sony TCN-767 cassette recorder for the Guatemalan specimens. Variation in tape speed was less than 5%. Tape analysis was done with a Kay Electric Co. Sonagraph audiospectrograph. Sounds were played into the Sonagraph at original tape speed. The Sonagraph voltage meter was kept at a level of -5 or below. At least 1, and usually many more, audiospectrographs were made and analyzed for each sound type of each species of beetle.

Field monitoring of logs occupied by *Odontotaenius disjunctus* (Illiger) in the United States and by *Passalus affinis* Percheron in the Dominican Republic was done by placing a microphone against the log. Logs chosen for field studies were small (7.5 cm to 20 cm dia. x 50 cm to 120 cm long) to facilitate log monitoring and tracing tunnel systems subsequent to monitoring. Once selected, the undisturbed log was monitored for spontaneous sounds; then a single beetle was introduced into the entrance of a passalid tunnel present in the log. The introduced beetle had been previously marked by engraving an identification number on the pronotum with an insect pin.

All 9 of the introduced beetles had been collected within 2 weeks of introduction, 5 on the same day they were introduced. All were handled only with gloves and forceps. After monitoring, tunnel systems were completely traced, all passalids collected, and the adults sexed. Field temperatures were measured in the air next to the upper surface of the log in the shade because it was impossible to locate a measuring device closer to an undisturbed passalid. Temperatures inside different parts of a shaded log will vary from the air temperature by as much as 6°C, depending on the time of day, with the air temperature changing much faster than the log temperature. This was determined in separate observations by use of a Bailey Instrument Co. BAT-4 Thermocouple indicator and 3 thermocouple probes.

RESULTS

Recordings were made of at least 1 kind of sound from 57 species in 13 different behavioral contexts. Species for which sounds were produced only in the disturbance context are not listed in Table 1.

Passalid sounds may be described in terms of pulses, bars, and phonotomes. The first 2 terms depend only on sound structure, whereas the latter requires knowledge of how the sound is produced. A pulse is a "wave train isolated or nearly isolated in time (discrete) when viewed with an oscilloscope" (Morris and Pipher 1972). A bar consists of a pulse or pulse train isolated from other sound by silences greater than 0.005 sec at 26°C (Fig. 1). Bars are usually the smallest unit of a passalid sound that a human hears distinctly. A series of bars produced at a constant rate with bars of approximately equal duration forms a simple bar train; at a varying rate and/or

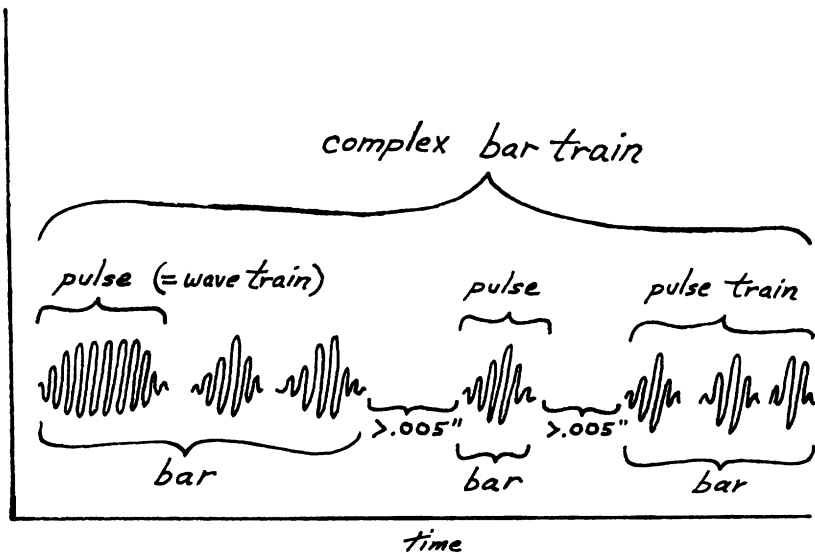


Fig. 1. Illustrated terminology of passalid sound units. A pulse may be produced by a single tooth-strike of the stridulatory apparatus; however, some pulses are apparently wave trains that are run together, produced by more than one tooth strike.

with bars of unequal duration, a complex bar train. The silence between bars in a bar train is usually less than 1 sec at 26°C, maximally 2 sec. A phonatome, in the sense of Walker and Dew (1972) and Leroy (1966), is the sound produced by a complete cycle of movement of the stridulatory apparatus (the abdomen, in adult passalids). Passalid sounds apparently contain no significant energy at ultrasonic levels; most energy is below 16000 HZ (Schuster 1975a).

I recognize 7 structurally distinct sound types produced by passalids (Fig. 2). Examples of actual audiospectrograms of each type are given in Schuster (1975a). These types are defined in the following key to adult passalid sounds at 26°C adapted from Schuster (1975a):

1. Bars longer than 0.06 sec; phonatome consists of 1 bar TYPE A
- 1'. Bars shorter than 0.06 sec; phonatome consists of 1 or more bars 2
- 2(1'). Complete sequence (all sounds produced in a given behavioral context) consists of 1 bar, or a series of bars produced in an irregular pattern TYPE D
- 2'. Complete sequence of sounds consists of a series of bars produced in a regular pattern 3
- 3(2'). Sequence composed of paired units, each unit (a bar or bar train) less than 0.05 sec long and interpair silences greater than 0.8 sec TYPE F
- 3'. Sequence composed principally of unpaired units, occasional paired units not as above 4
- 4(3'). Phonatome consists of 1 bar; sequence a simple bar train TYPE B
- 4'. Phonatome consists of more than 1 bar; sequence a complex bar train 5
- 5(4'). Eighty percent or more of bars longer than 0.01 sec TYPE C
- 5'. Eighty percent or more of bars shorter than 0.01 sec 6
- 6(5'). End of phonatome with 2 or more bars longer than 0.01 sec TYPE G
- 6'. End of phonatome with at most 1 bar longer than 0.01 sec TYPE E

Interspecific and intraspecific variation in sound types does exist but variation of a given sound type falls within the range of variation given in the key. One of the greatest interspecific variations of a given sound type is illustrated by the exceptional Type C sound produced by *Odontotaenius zodiacus* (Truqui) during aggression. Its phonatome is 0.31 to 0.41 sec long at 25°C and consists of 15 to 25 closely spaced bars. It has been heard on various occasions produced by at least 3 males. The 13 other species known to produce Type C sounds during aggression exhibit phonatomes lasting 0.09 to 0.39 sec at 25°C with from 4 to 14 bars/phonatome. Their bar production rate is less than 0.67 of that of *O. zodiacus*. In spite of being so different from Type C sounds produced by other species these of *O. zodiacus* are still easily recognized, even by ear, as Type C sounds.

A given sound type in a given behavioral context forms an acoustical signal. The same basic signal may occur in various species, e.g., most passalids make a Type A disturbance signal (Schuster 1975a). Previous workers have described 7 acoustical signals for the family (Alexander et al. 1963, Baker 1971, Schuster and Schuster 1971, Meyer-Rochow 1971). These plus the ones I have observed now total at least 31 signals (Table 1). This

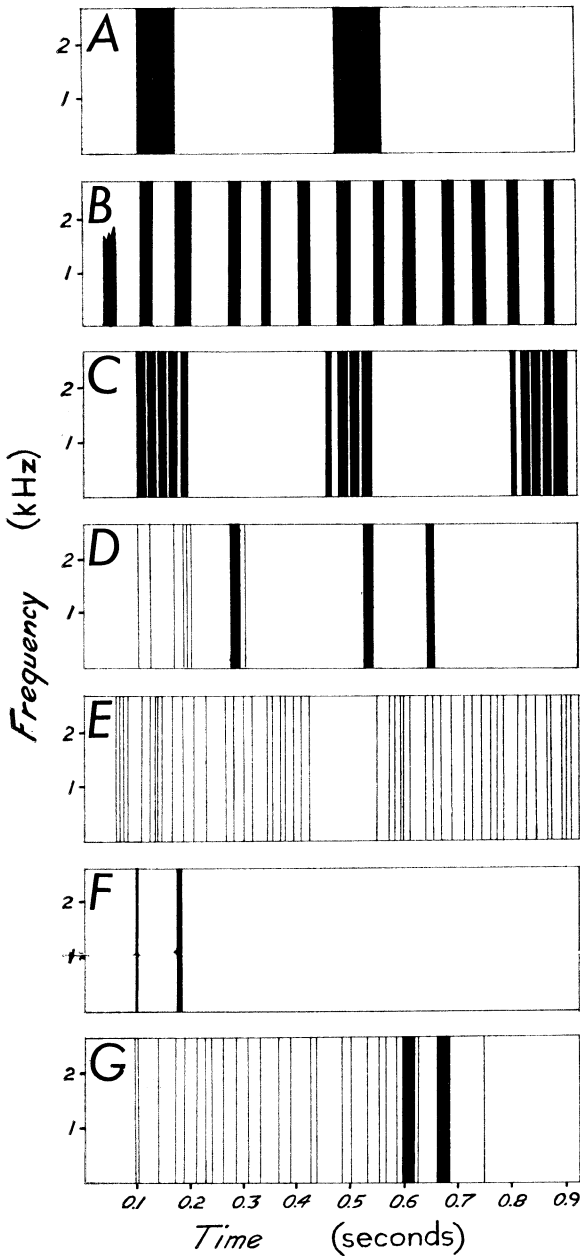


Fig. 2. Sound types produced by Passalidae. Semi-diagrammatic drawings of audiospectrograms: Type A—(female courtship signal, 30°C), Type B—(female aggressive signal, 29°C), Type C—(male courtship initiation signal, 29°C) all *Passalus punctatostriatus*; Type D—(mild aggressive signal, 30°C), Type E—(male aggressive signal, 30°C) both *P. punctiger*; Type F—(post-aggression signal during “push-ups”, 25½°C) *P. convexus*; Type G—(signal produced while feeding alone, 28°C) *P. punctiger*.

TABLE 1. SOUND TYPES OBSERVED IN 13 BEHAVIORAL CONTEXTS FROM 32 SPECIES OF THE 2 TRIBES OF NEW WORLD PASSALIDAE. THE BEHAVIOR CONTEXTS ARE: 1) COURTSHIP INITIATION; 2) COURTSHIP MALE ROLE; 3) COURTSHIP, FEMALE ROLE; 4) POST-COPULATION; 5) STRONG AGGRESSION, MALE AGGRESSOR; 6) STRONG AGGRESSION, FEMALE AGGRESSOR; 7) STRONG AGGRESSION, AGGRESSEE; 8) MILD AGGRESSION; 9) POST-AGGRESSION PUSH-UPS; 10) ALONE, FEEDING; 11) ALONE, WALKING; 12) ALONE, INACTIVE; 13) DISTURBANCE. PARENTHESES INDICATE THAT THE SOUND IS RARE, NOT ALWAYS OCCURRING IN THAT BEHAVIORAL CONTEXT; — = NO SOUND; * = SOUND OBSERVED IN INTERSPECIFIC AGGRESSION; # = SOUND PRODUCED BY FEMALE. FOR DESCRIPTION OF SOUND TYPES SEE FIG. 1. FOR MORE PRECISE CHARACTERIZATION OF BEHAVIORAL CONTEXTS SEE SCHUSTER (1975a) AND SCHUSTER (1975b).

Species	Behavioral Contexts												
	1	2	3	4	5	6	7	8	9	10	11	12	13
PASSALINI													
<i>Passalus (Pertinax) inops</i>											(B)		A/CB
<i>P. (P.) affinis</i>	C	A		A	CE	BE	A						A
<i>P. (P.) caelatus</i>	C	A											A(C) (F)
<i>P. (P.) convereus</i>	C	A	A			B	A	A	F			E	A
<i>P. (P.) dominicanus</i>							A				(B)		A
<i>P. (P.) punctatostriatus</i>	C	A	A		C	B						E	AB
<i>P. (Mitrorhinus) spinifer</i>	C	A											AB
<i>P. (Passalus) confjerus</i>	C	A	A		C								A
<i>P. (P.) elfriedae</i>	C	A			C								A
<i>P. (P.) interruptus</i>	C	A			C	E*							A
<i>P. (P.) interstitialis</i>	C	A			C	(E)	(B)*						AB
<i>P. (P.) jansoni</i>						E*							A
<i>P. (P.) punctiger</i>	C	A	A	A	CE(B)			DE		G		D	A
<i>P. (P.) near toriferus</i>	C	A			E*								A
<i>Spasalus crenatus</i>					C								A(C)
PROCULINI													
<i>Chondrocephalus</i> sp. n.	C	—	—										A
<i>C. granuliferus</i>	C		(A)										A
<i>Popitius eclipicus</i>	C	C	A					E			B		

total does not include larval acoustical signals, present in all species. For *Odontotaenius disjunctus* (Ill.) (formerly *Passalus cornutus* Fabr. and *Popilius disjunctus* Illiger, the common passalid of the Eastern U.S.), I have observed 5 sound types in 11 contexts, for a total of 14 different signals, the most known for any passalid species.

DISCUSSION

Adult passalid acoustical signals can be arranged in 4 general behavioral categories: 1) mating sequence, 2) aggression, 3) disturbance, and 4) other solo, i.e., signals produced in other contexts when not contacting another individual.

The mating sequence consists of 4 stages: 1) courtship initiation, 2) courtship, 3) copulation, and 4) post-copulation (Schuster 1975b). Copulation is not listed in Table 1 because sounds normally do not occur during this stage. Courtship-initiation and post-copulatory sounds are, in most cases, produced by the male. Females of some passalid species produce an acoustical courtship signal. Cerambycidae (Michelsen 1966) and Scolytidae (Wilkinson et al. 1967) are the only Arthropoda previously known to produce acoustical female courtship signals.

Aggression may be categorized as either strong or mild (Schuster 1975a). In the former, either sex may aggress with behavior essentially the same, but sound type produced differing between the sexes. The aggressor sometimes produces a signal which is apparently not sex dependent. Mild aggression is also apparently not sex dependent. In one species, *Passalus convexus* Dalman, a characteristic post-aggression signal occurred.

Disturbance sounds may be elicited by manipulating or blowing on a beetle. In nature, they are produced when the beetle is attacked by a predator and, at least in the case of attack by crows (Buchler et al. 1981), have a deterrent function. They may be homologous to the signal produced by the aggressor mentioned above.

Sound is produced in contexts not directly related to mating, aggression, or disturbance. It is occasionally heard when the beetle is not in direct contact with another individual, while it is feeding, walking, or inactive.

On the basis of acoustical signals, New World passalids may be divided into two groups: species with, and species without, a male courtship signal (Table 1). The species that lack the signal are all members of the New World tribe Proculini, but other Proculini and all Passalini in which courtship has been observed possess the male courtship signal. This implies that, since the Proculini may be derived from the pantropical Passalini, the acoustical courtship signal was secondarily lost in some Proculini.

The presence of similar signals in members of both tribes of the subfamily Passalinae suggests an early evolution of the major components of the acoustical repertoire. Acoustical signals of the Old World subfamily Aulacocyclinae, are virtually unknown.

The interspecific similarity of passalid acoustical signals is in contrast to the variety found in some insect groups. For example, in Orthoptera and Cicadidae, acoustical calling signals are the primary means of long-distance sex-attraction. The development of species-specific differences in such signals is selectively advantageous in areas of sympatry because they will bring together only conspecifics. In Passalidae, acoustical calling signals are un-

known. Many do have courtship signals, however, and it has been postulated that, in closely related species together occupying restricted niches (e.g., dung, rotting logs), courtship signals, rather than calling signals, should evolve toward species-specificity due to the high probability of chance encounter between males and females of different species (Alexander et al. 1963). In Passalidae, up to 10 species may occupy the same rotting log (Luederwaldt 1931), yet courtship-initiation and courtship signals (as well as other signals) appear similar among various species, at least in being composed of the same basic sound types (Types C and A, respectively, being the most common). However, I have never found the tunnel systems of 2 species definitely interconnecting, even though approaching within 1.5 cm of each other. Sound might function in preventing beetles from tunneling into areas occupied by other species (and conspecifics?), similar to what apparently occurs intraspecifically in *Dendroctonus* beetles (Scolytidae) (Rudinsky and Michael 1973). That interspecific recognition occurs without sound mediation when passalids are in direct contact is suggested by strong, but silent, aggression in 0.5 of 14 laboratory mixing experiments in which aggression occurred (Schuster 1975a). Intraspecific aggression is usually accompanied by sound.

In nature, pheromones may play an important role in interspecific recognition. *Dendroctonus* use both sound and pheromones in communication. Nothing is known concerning passalid pheromones, though I have noted a distinct odor associated with *O. disjunctus*, *Verres hageni* Kaup, *Proculus mniszewski* (Kaup), and *Veturius platyrhinus* (Westwood).

An interesting example of convergent evolution is seen in certain structural similarities of passalid signals with those of *Dendroctonus*, a genus of wood-inhabiting beetles with a high level of social behavior and a large sound repertoire. In *D. pseudotsugae* Hopkins and *D. ponderosae* Hopkins, as in passalids (and many other organisms), courtship begins with behavior quite similar to aggression, then switches to the decidedly different courtship behavior (Rudinsky and Ryker 1976, Ryker and Rudinsky 1976). The sounds also reflect this change. During aggression and courtship-initiation, males of *Dendroctonus* and Passalidae produce an interrupted sound composed of distinct subunits (Type C in Passalidae, Fig. 1). Switching to courtship, the male changes its sound type to 1 without distinct subunits, in both Passalidae (Type A, Fig. 1) and *Dendroctonus* (Ryker and Rudinsky's uninterrupted chirp). In certain crickets, aggressive signals and courtship *interruption* signals are similar (Alexander 1962); on passing to courtship, a structural change occurs, but it is not parallel (interrupted to uninterrupted sounds) to the changes occurring in Passalidae and *Dendroctonus*. The similarity in courtship between Scolytidae and Passalidae extends to copulation; they are the only beetles known to copulate venter to venter (Schuster 1975b).

Presumably, the high level of sociality and similar mating positions of passalids and some scolytids are adaptations to the similar concentrated resource microhabitat they inhabit (tree trunks) (Wilson 1971). Social insects are known for their elaborate communication and advanced subsocial insects tend to have advanced repertoires e.g., *Anurogryllus muticus* (now called *A. arboreus*), the cricket with the greatest number (6) of acoustical signals (Alexander 1962) is also highly subsocial (West and Alexander 1963).

Alexander (1966) stated that *A. muticus* possesses "a greater variety of acoustical signals than is known for any other kind of insect, or for any

fish, amphibian, or reptile, and even many birds". Despite differences in our respective ideas as to what constitutes a given signal, it appears that the passalid *O. disjunctus* has the largest acoustical repertoire known for a species of arthropod. This advanced repertoire is correlated with the highest degree of social behavior known outside the Isoptera and Hymenoptera in which passalids help their parents in the care of sibling pupal cases (Schuster and Schuster, in preparation).

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