COMPARATIVE BEHAVIOR, ACOUSTICAL SIGNALS, AND ECOLOGY OF NEW WORLD PASSALIDAE (COLEOPTERA)

BY

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Behavioral and life history studies, including laboratory and field experiments, were made of the subsocial family Passalidae. Rotting logs are colonized by either a single male or female black adult that is subsequently joined by a member of the opposite sex. Both members of an established pair aggress against another individual of either sex when it is introduced into their tunnel system. The evolutionary advantage of a beetle attacking a member of the opposite sex may result from high juvenile mortality in the presence of non-related adults. Adult passalids sometimes live more than 2 years and produce more than 1 brood. Cooperative care of juveniles by parents and the continued residence of adult offspring in the tunnel system with their parents characterize the Passalidae at a stage between primitive subsocial and truly social behavior. Up to 10 species may occupy the same rotting log, apparently without connections between their respective tunnel systems.

Many species occur in wet tropical forests; few occur in desert and temperate regions or at altitudes above 2800 m. Seasonally synchronized life cycles are associated with seasonal cold or dryness. Acoustical signals recorded from adults of 42 species belong to 7 structural sound types. The signals occur during the mating sequence, aggression, disturbance, and other situations. Larvae stridulate in at least 3 behavioral contexts. In 1 species, Odontotaenius disjunctus, adults produced 5 of the 7 sound types in 11 behavioral contexts for a total of 14 acoustical signals, i.e., sound type-context combinations, more than is known for any other arthropod species. Passalid signals differ little among species, much less for example, than the signals of Orthoptera. Passalids are notable in that females as well as males make a variety of signals.

INTRODUCTION

Passalids are subsocial* beetles that have an elaborate system of sound communication. For example, I have discovered more kinds of acoustical signals for one species of passalid than are known for any other arthropod species. This paper compares acoustical signals and behavior within the family, and presents life-history information, in anticipation that this will provide a basis for studies of the evolution of social behavior and communication.

Little has been reported previously concerning the behavior of passalids, despite their ubiquitous occurrence in rotting wood over much of the world. Reyes-Castillo (1970) summarized the literature on the behavior and ecology, as well as other features, of Passalidae. He also included habitat data, where known, for each New World genus. Gray's paper (1946) on *Odontotaenius disjunctus* is the most comprehensive work on the biology of a single passalid species.

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*Subsocial insects are those that care for their own nymphs or larvae but lack one or more of the following characteristics: cooperative brood care, reproductive castes, and overlap between generations. The latter characteristics when found together delineate the truly social, or eusocial, insects (e.g., bees, ants, termites) (Wilson, 1971).

The small size of the family, about 500 spp. compared to, for example, 30,000 spp. in the Scarabaeidae (Woodruff, 1973), is conducive to a comparative study of behavior. The family contains 2 subfamilies, according to the most recent taxonomic revision (Reyes-Castillo, 1970). Only Passalinae occurs in the New World where it is represented by 2 tribes, the Passalini which is pan-tropical and the Proculini which is Neotropical except for *Odontotaenius disjunctus* (Illiger). This species, formerly known as *Passalus cornutus* Fabricius and *Popilius disjunctus* Illiger, occurs in the eastern United States. The relatively large size and slow movements of passalids facilitate observation, as does the fact that they can be easily maintained in the laboratory. Since most species are tropical and live in rotting wood, the widespread cutting of the world's forests, particularly in the tropics, may result in a temporary increase in size of some passalid populations. Subsequently, however, the final elimination of the wood may result in extinction for many species. These facts suggest that now is the opportune time for investigation of Passalidae.

BIOGEOGRAPHY, ECOLOGY, AND LIFE CYCLE

Range

Passalidae are primarily pan-tropical. The northernmost record I have found for any passalid is for *Odontotaenius disjunctus* in Saginaw Co., Michigan. In the southern hemisphere, one species, *Pharochilus politus* (Burm.), occurs in Tasmania (Dibb, 1938) and a number of species are found in northern Argentina. I examined temperate forests in Chile and found no evidence of Passalidae. The record of *Passalus convexus* Dalman from Chile (Luederwaldt, 1931) is probably erroneous. The forests of southern Chile, as well as those of the Pacific Northwest of the United States, lack passalids and are separated from the nearest passalid populations by extensive dry regions. Passalids may never have inhabited Chile; however, the only fossil known for the family is from the Oligocene of Oregon (Chaney, 1927). The New World passalid fauna extends into the Pacific with *Popilius lenzi* Kuwert on Costa Rica's Isla del Coco (Van Doesburg, 1953) and *Passalus interruptus* (L.) in the Galapagos Islands. Only the Passalini are represented in the West Indies (Reyes-Castillo, 1970).

The greatest diversity of species within the tribe Proculini occurs in the mountains of Mesoamerica and northern South America, whereas the greatest diversity of New World Passalini is found in South America.

Although Blackwelder (1944) lists the familiar *Odontotaenius disjunctus* as occurring as far south as Brazil, its range is actually Ontario, Canada, and the eastern United States (Reyes-Castillo, 1970, 1973). In the United States, it occurs north to Massachusetts and Michigan, south to central Florida and west to Kansas. Reyes-Castillo and I have examined many of the world's major collections and have collected in most of the countries for which it has been cited and have yet to encounter a specimen from outside this range.

Macrohabitat

Passalids occur most commonly in moist forests. Both species and individuals are abundant in tropical rain forests (near Tingo Maria, Peru, 1 of every 3 or 4 logs contained passalids) and quite common in montane forests such as the cloud forests, pine forests, and pine-oak forests of Mesoamerica. They are less abundant in the drier, tropical deciduous forests (near Cañas, Costa Rica), only 6 of 150 to 200 logs contained passalids. A few species occur in savanna (Reyes-Castillo, 1970). *Odontotaenius disjunctus* inhabits northern temperate deciduous forests, including the relatively dry turkey-oak sandhills of north central Florida. One species, *Ptichopus angulatus* (Percheron), is symbiotic with leaf-cutter ants in desert and forest regions.

Passalids are not found in regions of prolonged cool temperatures such as occur at latitudes greater than 45° or on tropical mountains above 3500 m. The diversity of species decreases as these extremes are approached. Only 2 species are found in north temperate regions where freezing temperatures and snow occur: *Cylindrocaulus patalis* Fairm. of Japan and *Odontotaenius disjunctus* of the eastern United States and Canada.

In the neotropical mountains, the few species of Passalidae that occur above 2800 m belong to the tribe Proculini and, as compiled from Reyes-Castillo (1970), are the following:

Chondrocephalus granulifrons	to 3300 m in pine forest of Guatemala
Vindex agnoscendus	at 2800 m in Mexico
Petrejoides recticornis	at 2860 m in Mexico
Petrejoides jalapensis	at 2800 m in Mexico
Undulifer inciscus	at 2800 m in Mexico
Pseudacanthus spp.	to 3000 m in southern Mexico
Odontotaenius striatulus (synonymous with *O. striatopunctatus*?)	at 2900 m in Ecuador
Publius crassus	to 3000 m

The only representatives of the New World Passalini known from above 2200 m are a species of *Passalus* that I collected at 2250 m on the Sierra Talamanca in Costa Rica and an undescribed species of Passalus that I found in a log with larvae and eggs at 2750 m in Ecuador.

In Peru (Tingo Maria region), I did not encounter passalids above about 2500 m even though areas examined contained many apparently suitable logs. In Costa Rica on the Cerro de la Muerte of the Sierra Talamanca, I examined 25 to 30 logs in an oak forest above 3000 m without finding passalids. All passalids collected on this mountain were collected below 2700 m. At 3000 m, the mean annual temperature (1962) was 10.8°C, the lowest temperature of the year (1963) was 00.0°C, and the highest was 24.5°C (Scott, 1966).

Microhabitats

Passalids are found in moist, decomposing plant material. Though I have found adults in dry rotting logs, I have encountered juvenile stages only in moist conditions. Gray (1946) showed in the laboratory that pupae of Odontotaenius disjunctus would not reach adulthood at relative humidities below 92% and that eggs would develop only in direct contact with water. Passalids are not generally found where flooding is frequent, such as along some river courses.

The commonest microhabitat of passalids is a rotting log. They occupy standing trunks as well as fallen ones. I found a species of Spasalus (near S. crenatus Macleay) at a height of 7 m in a standing trunk near Iquitos, Peru. D. Minnick has informed me that he collected a group of O. disjunctus more than 6 m above the ground in a standing trunk in Marion Co., Florida.

Tunnels may occur in one area of a log and not in another. I observed tunnels of the Spasalus sp. mentioned above not to cross certain fungus lines in the wood (probably an ascomycete). They occurred primarily in areas through which the fungus had apparently already penetrated.

Most species occur in dicotyledenous wood, though many occur in conifers (e.g. Pinus, Araucaria) and a few are found in palms (Reyes-Castillo, 1970). Some species are more restricted than others. For example, O. disjunctus is found in dicotyledenous wood but seldom in pine (Savely, 1939), whereas O. striatopunctatus (Percheron) is commonly found in both. Up to 10 species have been encountered in a single log (Luederwaldt, 1931). Flatter species tend to be found under bark (e.g., Passalus interstitialis Esch.), more convex species deeper in the log (e.g. P. convexus Dalman).

A few species of Passalidae are found in other microhabitats. Passalus punctiger Lepeletier et Serville have been found under cow manure in Brazil, and larvae, pupae, and adults of P. dubitans (Kuwert) have been collected under epiphytic bromeliads in Brazil (Luederwaldt, 1931). J. G. Edwards and R. Mains (pers. comm., 1972) collected

Passalidae under stones in the Yucatan Peninsula. J. Hendrichs and P. Reyes-Castillo (1963) discovered that *Ptichopus angulatus* is commonly found in the detritus associated with nests of the leaf-cutter ant *Atta mexicana*, both in the wet forest regions and in the drier desert regions of Mexico. In excavating these ant nests in a desert of Hidalgo, Mexico, Reyes-Castillo and I found passalid larvae and adults together 30 cm deep in the detritus of the ant nest. Despite the general dryness, this section of the nest had visibly greater moisture and the detritus was well packed so that passalid tunnels were easily visible as we excavated.

In Peru, during 1970 and 1971, I found evidence of passalids in a particularly unusual habitat: limestone caves. Near the town of Tingo Maria is a large cave, known locally as the "Cueva de las Lechuzas." Its mouth is about 18 m in diameter and the first chamber is about 30 m wide. Within it lives a large colony of oilbirds, *Steatornis caripensis* Humboldt. These birds feed on fruits, especially of palm (*Bactris gasipaes* H.B.K.) which they bring into the cave (Dourojeanni & Tovar, 1972). The seeds are dropped on the floor. This, as well as excrement from the birds and from bats, provides nutrients for a large arthropod fauna within the cave. The most abundant arthropods to the unaided eye are a large black species of tenebrionid beetle, a small species of lygaeid bug, and large cockroaches of the genus Blaberus. Amid the remains of insects which litter the floor of the cave, I observed many pieces of passalid exoskeletons, especially elytra. They appeared to be most common about 45 m from the cave mouth, but were found as far back as 200 m from the entrance. In a 360 cm^2 area 20 m from the entrance, I counted remains of 19 individual passalid beetles. Though I saw no living passalids in the cave, Dourojeanni (pers. comm., 1973) noted live passalids, adults and larvae, there in 1961, and he suggested that they lived on the decomposing seeds brought in by the birds (Dourojeanni and Tovar, 197?).

I noted passalid remains in 3 other caves in which oilbirds live or formerly lived in that region of Peru. However, I found similar remains under an overhanging cliff (margin of cliff extended about 3 m beyond the base and formed a grotto about 9 m wide), and in a small cave (entrance diameter 3 m). In neither were there oilbirds or evidence, such as palm seeds on the floors, that oilbirds had ever occupied them. Both sites are located in southern San Martin province near the village of Aspusana. In no case did I find an entire passalid or a living beetle, only pieces. Most of the insect remains in the cave were concentrated under a small ledge about 50 cm above the cave floor. Seventy-five percent (57 individuals) of the arthropods represented were passalids. There were remains of 32 individuals of Passalus interruptus (L.) as well as remains of 2 other species of Passalus and a species of Veturius, probably V. platyrhinus (Westwood). The only other insects represented by remains of more than one individual were 7 ponerine ants and 4 Rhinostomus barbirostris (Fabricius), a large curculionid. P. interruptus and V. platyrhinus are among the commonest passalids collected in this region of Peru. Since there was very little, if any, decomposing plant matter in this cave, I am forced to conclude that the beetles were brought into it, perhaps by bats or rodents, and then collected, possibly by the latter, under the ledge. The high proportion of passalid parts, predominantly elytra, might be explained by the fact that they are quite glossy and may be more attractive to acquisitive rodents than pieces of other insects they eat or find. Perhaps such collecting contributed to the passalid remains in the oilbird caves as well.

Stages

The life cycle from egg to adult requires about 2 1/2 to 3 months, based on Gray's study (1946) of Odontotaenius disjunctus and my observations of Passalus affinis and P. punctiger. Passalid adults remain with their offspring throughout development so that it is possible to find 2 generations of adults in the same tunnel system. This overlap between generations is one characteristic in the development of social behavior, according to Michener (1969). Other characteristics listed were cooperative brood care and reproductive castes. Passalid parents cooperate in raising the juveniles by providing frass, which serves as food for the larvae, and by assisting the larvae in the construction of the pupal cases. Whether the adult progeny aid in rearing their siblings is unknown, though Miller (1932) claimed that the parents keep the teneral adults away from the pupal cases in *O. disjunctus*. Reproductive castes have not been shown to exist in Passalidae. According to Wilson's (1971) adaptation of Michener's classification, passalids have intermediate subsocial behavior.

Eggs

Passalids take a number of days to lay a clutch of eggs in a restricted portion of the tunnel system, the "nest." Gray (1946) stated that *Odontotaenius disjunctus* generally lays only 2 to 4 eggs in a 24-hour period. My observations of various tropical passalids, both in the field and in the laboratory, also indicate a prolonged egg-laying period. Eggs possibly are carried to the nest after being laid. Gray observed individuals of *O. disjunctus* carrying eggs in their mandibles. When I placed eggs and adults in a petri dish, similar behavior was displayed by *O. zodiacus* (Truqui) and *Passalus punctiger*. In the nest, the eggs are in the midst of fine frass. The nest dimensions range from 75 x 50 mm to 13 x 13 mm. Gray notes that there are usually 20 to 35 eggs, with a maximum of 60, in a nest of *O. disjunctus*. The maximum number of eggs laid in a special laboratory rearing chamber by a *P. punctiger* was 20. Of 11 natural nests of tropical passalids I examined, the greatest number of eggs found was 12 in a nest of *P. convexus*. Gray noted that the eggs of *O. disjunctus* change color as they develop, from bright red through brown to dark green. This appears to be the case for other passalids as well. I observed both red and green eggs in nests of *Verres hageni* Kaup in Costa Rica and *P. caelatus* Erichson in Peru. Eggs of *O. disjunctus* hatch in about 16 days at 27°C (Gray, 1946).

Larvae

Passalids have 3 larval instars, easily distinguished by differences in head width. First instar larvae of many species have more long setae, especially on the notum and dorsal abdomen, than later instars. Early first instar larvae in rearing trays with their parents usually remain within 4 cm of the egg nest, as evidenced by the distribution of their characteristic disc-shaped fecal pellets. Larvae are generally gregarious and are often found with an adult, occasionally several in a line with their heads under its body.

The principal larval foods are frass and fecal pellets. First instar larvae feed on the fine frass around the eggs. Third instar larvae also tear pieces from large wood chunks. Ohaus (1900) indicated that wood must be prepared by the adult. Pearse et al. (1936) studied the food requirements of *O. disjunctus*. This work was aptly criticized by Gray (1946) for lack of controls and for not considering the effect of diet on larval ecdysis. Gray concluded that larvae are best reared on wood triturated by the adults.

The durations of each larval stadium, about 12 days, for *Passalus punctiger* and *P. affinis* appear similar to those given by Gray (1946) for *O. disjunctus*.

Pupae

The third instar larva pupates in a case constructed with the aid of adults. About 5 days prior to pupation, the larva ceases feeding, becomes whiter, and enters a prepupal stage. In the absence of adults, the prepupa will roll over and over, forming a depression in the frass in which it pupates. If adults are present, they will aid the larva in the construction of a pupal case of fine textured, compact frass, and excrement (Figs. 1-3) as described by Miller (1932) for *Odontotaenius disjunctus*. Only one adult need be present for pupal case construction, as was observed in a petri dish containing only the larva and an adult female of *Passalus affinis*. The duration of the pupal stage of *O. disjunctus* is 10 to 12 days Gray (1946). Casual observation of 7 pupae belonging to 4 tropical species, *P. affinis*, *P. punctiger*, *Spasalus crenatus*, and *Popilius* near *refugicornis* Burnheim, indicated little difference in pupal duration from that of *O. disjunctus*. All

Fig. 1. Passalus punctiger--pupal cases in laboratory rearing trays.

Fig. 2. Passalus punctiger--pupal case containing prepupa.

Fig. 3. *Passalus punctiger*--pupal case containing pupa.

pupal durations were less than 20 days, with 4 less than 16 days.

Teneral Adults

At ecdysis, the new adult is very soft and has white elytra, with the remaining body orange. After about 3 hours, the elytra have a noticeable orange tinge. About 1 1/2 days later, the bright orange adult emerges from the pupal case. Adults blacken--the dorsum first, the venter last--at varying rates. Some may be completely black after only a few weeks, while others take many months. In the case of 4 individuals of *Odontotaenius striatopunctatus* collected as red adults and maintained in the laboratory, the elytra turned black but the venter was still a dark maroon after 2 years.

Young adults are not sexually mature. Virkki (1965) reported that they have spermatogonia but lack spermatozoa. He did not state when the adults became sexually mature. I observed courtship behavior 3 months after pupal ecdysis of the male and female in *Passalus punctiger* and 4 months after ecdysis of both sexes in *O. disjunctus*, which may indicate maturation by this time.

Mature Adults

Black adults migrate from one log to another by walking or flying. Most individuals found outside logs are fully black, or nearly so, with black elytra and blackish-maroon venters. In a study of Odontotaenius disjunctus, 61 of 62 individuals found in recently colonized logs were completely black; the single exception possessed a blackish-maroon venter and black elytra.

Adults are occasionally encountered outside logs. An individual of O. disjunctus discovered in the middle of a dirt road at 11:04 a.m. on 26 January 1974, near Gainesville, Florida, walked for 35 min, traversing approximately 20 m, before finally entering an old passalid tunnel in a log. During the entire period, the beetle traveled in approximately a straight line, walking into the wind. The antennae were extended nearly straight forward and raised about 10° from the horizontal. While on the road, it traversed 120 cm in 1 min; when crossing leaves on the forest floor, it traveled 60 cm/min. Another O. disjunctus, observed walking from 4:45 to 6:50 p.m. on 27 September 1963, near Ann Arbor, Michigan, also tended to travel in straight lines. This beetle ascended and descended the trunks of 2 trees to heights of 55 cm and 95 cm respectively. Occasionally while on the tree trunks it would release its grip on the bark with its front legs and stand with its prothorax and head extended away from the trunk. Its rate of walking across the forest floor was 38 cm/min. An individual of Passalus interruptus was observed at 9:50 a.m. on 2 October 1970, in Tingo Maria, Peru to walk in a straight line for 3 m at a rate of 16 cm/min.

Passalids have been observed flying, though uncommonly, and have been caught at sites to which they must have flown. Some species have reduced wings and are incapable of flight (e. g. Proculus spp.). Most flights apparently occur at night. I observed an individual of Passalus punctiger under a street lamp at 7:37 p.m. on 5 May 1970, in Tingo Maria. While on the ground it raised its separated elytra, then flew upward about 1/2 m before crashing to the ground approximately 1 m from where it took off. In Costa Rica during March 1967, passalids were caught in mist nets 1 to 2 m above the ground. An individual of Passalus jansoni was caught between 9:00 and 10:30 p.m., and 3 individuals of P. punctiger were caught, 1 between 9:00 and 10:00 p.m., 1 between 10:00 p.m. and 12:00 a.m., and 1 between 3:00 and 5:00 a.m. Gray (1946) doubted that Odontotaenius disjunctus could fly and went so far as to drop adults with elytra unhooked and wings spread from tall buildings to test their flightlessness. Nevertheless, J. E. Lloyd caught one at dusk while it was flying (pers. comm., 1974), and D. Mays saw one fly to a black light (pers. comm., 1975). Five other beetles, all female, were either seen flying, or found in situations to which they had probably flown, by T. J. Walker and R. Walker (pers. comm., 1973, 1974).

In order to study colonization, unoccupied logs were examined periodically. Ten water oak (Quercus nigra) logs of roughly the same size (8 to 19 cm diameter, 43 to 86 cm length) were placed 6 m apart. They were examined on the average every 17 days beginning 22 October 1972 for 2 years. All newly colonizing beetles were removed when found. Logs were replaced when damaged by excessive colonization or forest animals. I neither collected passalids nor disturbed other occupied logs within about 500 m of the experimental site. The logs were located in a mesic hammock near Gainesville, Florida, an area with a large population of _O. disjunctus_. The oak logs employed had been dead and cut for 17 months and had never been occupied by passalids at the time the experiment began, though other logs of the same age had already been colonized. This indicates that colonization occurs sooner in Florida than in North Carolina, where, according to Savely (1939), logs are at least 2 years old before passalids enter them. Sixty-two beetles came to the logs. Twelve were found alone in new tunnel systems, indicating that beetles arrive singly at a new log and begin a tunnel system. Of these, 8 were females and 4 males, demonstrating that the first arrival may be of either sex. The remaining 50 beetles were found as male-female pairs. The second beetle, therefore, probably arrives within a few days after the first. The evidence does not eliminate the possibility that some colonies could have been initiated by a male and a female together but renders it unlikely.

In order to determine what occurs when a second beetle enters an occupied tunnel system, introduction experiments were performed with individuals of Odontotaenius disjunctus which had not yet migrated and with individuals that had recently migrated. Adults which had not yet migrated were obtained by using offspring reared to adulthood by pairs of beetles in field cages. These emerged from pupation approximately 1 1/2 months prior and were black or nearly black at the time of the experiment. They had never contacted passalids other than their siblings or parents. Offspring from 2 such families were employed. First, 8 offspring, 2 males and 2 females from each family, were isolated in the laboratory. Individuals of one family were placed in terraria, those of the other in petri dishes. After 3 days, a small log less than 30 cm long was added to each terrarium. Three days later, a beetle from a petri dish was introduced into a terrarium, in each possible combination, i.e. a male to a female, a female to a male, a male to a male, and a female to a female. In the 2 cases where a beetle was introduced to another of the same sex, the intruder was attacked by the occupant, which produced an aggressive sound characteristic of its sex. The 2 male-female combinations did not result in aggression or sound production, though courtship was observed in one case in December, 4 months later. Lack of courtship behavior earlier might have resulted from sexual immaturity.

Beetles which had recently migrated were obtained from the logs examined periodically for colonization. Individuals which were found as the sole beetle in a tunnel system were used in 2 introduction experiments. The first was an attempt to introduce a female into a log occupied by another female. The female being introduced could not be forced to enter the tunnel. Since the tunnel was only 10 cm long, she probably had contacted the rear of the occupant beetle and in some way determined the tunnel was already occupied by another female.

In the second experiment, a male and a female, each collected as the only beetle in a new colony on 6 October 1973, were kept isolated until 8 November, when the female was placed into the male's petri dish. Contact was followed by antennal vibration and the brief (6 sec) production of male and female aggressive sounds. Courtship sounds began 83 sec after the first contact. Copulation occurred 80 min later.

Imagos reproduce during their first year of adulthood. This was ascertained by placing a pair of red adults in a field cage which was covered with bronze screening. The cage was rectangular, 61 cm tall and 1655 cm^2 in cross-section, and framed by 2.5 cm x 5 cm lumber treated with copper arsenate. A board frame was attached to the open bottom to extend 15.2 cm into the soil. The male had been collected as a larva in June and the female as a red adult in July, 1973. On 5 August 1973, they were placed in the cage and provided with moist, rotting oak wood. On 5 May 1974, first instar larvae were found with the pair, which still had not completed their first year of adulthood.

Adults produce more than one clutch of eggs. In the laboratory, a pair of *Passalus affinis* produced 2 clutches 3 months apart, and a pair of *P. punctiger* produced 3 clutches, each separated by 3 months. Larvae were reared from all but the second clutch of *P. punctiger* eggs, which I had disturbed. Reproduction by a single pair appears to be almost continuous in the field in certain climates. Eggs and pupae were found 3 cm apart in a tunnel system occupied by a black adult male and female of *Verres hageni* in Costa Rica.

Adults may live more than 2 years in the field. Presently, I have field cages that have contained the same adults of *Odontotaenius disjunctus* for 1 1/2 years. I have had adults of various species live longer than 2 years in the laboratory. Of these, individuals of *Passalus punctiger* were still reproducing after 2 years.

The number of adults found in a single tunnel system varies. Occasionally, one may find a single beetle in a short tunnel, obviously recently arrived. Frequently, a system contains just 2 adults. In logs that have been colonized for a long period, there may be interconnections between different colonies. Generally, when more than 2 beetles are found in the same system or same area of a large system, they are probably the original colonizing pair and/or their immediate offspring. This is indicated by the teneral reddishness often present in many individuals of larger groups.

I have never observed the tunnel systems of different species to interconnect. What happens when tunnel systems of 2 species meet may be similar to the reactions in certain mixing experiments: An individual of Passalus interruptus was introduced into a container of 3 Veturius platyrhinus. It aggressed against all 3 Veturius. The first P. interruptus was removed and another introduced. Upon contacting the Veturius, the new Passalus rapidly broke contact. Two of the Veturius aggressed against it. The behavior of these 2 Veturius was unlike any previously noted. When one contacted P. interruptus, it would back up, lower its head, bulldoze forward, then lift the head. This resulted in piling of frass and pieces of wood against the P. interruptus. At least 8 separate sequences of this behavior were observed. Perhaps in this manner accidental linkages between tunnel systems are blocked. This bulldozing behavior seems similar to that described by Miller (1932) for Odontotaenius disjunctus adults during pupal case construction.

Periodicity

Passalid life cycles were examined in warm, moist areas having relatively little fluctuation in either temperature or moisture throughout the year (Tingo Maria, Peru; Osa Peninsula and Arenal, Costa Rica), in an area with a pronounced dry season (Cañas, Costa Rica), and in areas with a pronounced cold season (northern Florida, Sierra Madre Oriental near Monterrey, Mexico). The Tingo Maria region (approximately 9° S. latitude), is a zone of Subtropical Wet Forest (Tosi, 1960). The precipitation is 3300 mm/year, August being the driest month, with 100 mm of rain. The mean annual temperature is approximately 24°C (Tosi, 1960). Adults collected at any time of the year were active. Life-cycle information concerning 6 of the commoner species of this region is presented in Table 1. Considering all of the species together, and assuming that development from egg to adult requires 2 1/2 to 3 months (p. 10), one can infer the presence of juvenile stages in all months of the year. Likewise, adults were occasionally observed flying or walking (apart from logs) throughout the year. Therefore, in the warm, moist environment of Tingo Maria, with minor oscillations of temperature and rainfall during the year, the life cycles of the various passalid species are probably aperiodic and are at least not synchronous.

Near Petropolis, Brazil, Ohaus (1909) observed that some species were aperiodic, with eggs, larvae, pupae, and

Table 1. The months in which were found the different life stages of 6 species of Passalidae in the region of Tingo Maria, Peru.

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Passalus caelatus	E A					A						
P. coniferus	L P A		A	A	A				A			
P. convexus		L P A		E L A	A		L A					
P. interruptus				A	A			A	L A			
P. interstitialis	A	A		L A					E L P A			
Veturius platyrhinus	A	E A		L P A		A			L A	A		

Note: E = eggs, L = larvae, P = pupae, A = adults. A blank for a given species in a given month indicates that species was not collected in that month.

red and black adults present at all times of the year. Other species were seasonal. They were found only as pairs of adults with or without eggs, in September and October at the commencement of the more rainy period.

In Costa Rica, at approximately 9° N. latitude, I collected passalids in tropical wet areas (Osa Peninsula and Arenal) and in Tropical Dry Forest (Cañas) during February and March, i.e. in the dry season. This dry season is most pronounced around Cañas in Guanacaste Province, where from December through March the monthly rainfall is less than 20 mm. The total yearly precipitation is about 1800 mm (Scott, 1966). The mean annual temperature in 1963 was 27.8°C; the lowest temperature recorded for the year was 20.0°C, and the highest was 36.5°C (Scott, 1966). Records for 1964 for the Osa region (Golfito) give the annual rainfall at 3800 mm, February having the lowest monthly total of 58 mm. That year's lowest recorded temperature was 21°C, the highest 35°C (Anonymous, 1967).

During the pronounced dry season near Cañas, adult Passalidae were mostly inactive. Of 7 specimens of *Passalus punctiger*, 5 had to be forcibly probed before they would show any movement. This inactive state was also seen in the 1 live specimen of *Verres hageni* collected there. This inactivity appears to be a response to dryness, since adults (n=19) of both of these species, when collected on the Osa Peninsula, were very active. In addition, adults (n=7) of *V. hageni* were similarly active at Arenal.

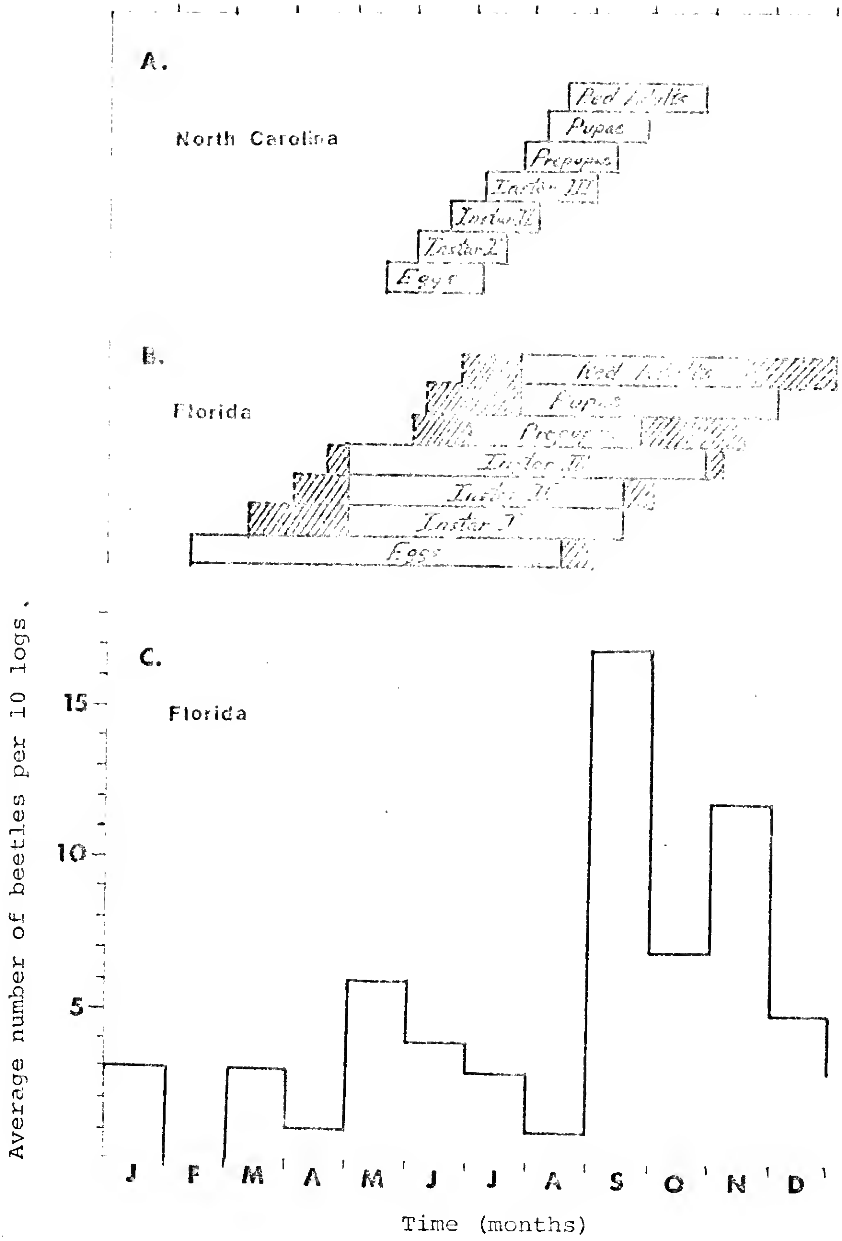
Juveniles were sought during the dry season. Near Cañas, examination of 150 to 200 logs yielded 9 live adults and 14 dead ones. No juveniles were found. Juvenile V. hageni were present at Arenal and the Osa Peninsula. At the Osa Peninsula, two species that were not found in the Tropical Dry Forest, Passalus jansoni and Veturius sp., were with eggs and/or larvae. This indicates that, in areas with a pronounced dry season, the unfavorable period is passed only in the adult stage.

Northern Florida, at 30° N. latitude, at the southern edge of the temperate deciduous forest of the eastern United States, has a pronounced cold season, often with frosts occurring from November through February. Odontotaenius disjunctus is the only passalid in this region. When encountered in wood on cold days, adults do not move and are extremely sluggish when manually disturbed. On warm days during the winter, however, adults are active when found.

The seasonal life history of Odontotaenius disjunctus in northern Florida (Fig. 4 B) was determined by examining 1 to 4 occupied logs every 2 to 3 weeks from October 1972 to September 1973, and on occasion for 1 1/2 additional years. Extrapolations beyond actual observations are based on laboratory studies of development time at 27°C by Gray (1946). The earliest red egg (recently oviposited) discovered was collected on 9 February 1974. Cooler winter temperatures probably retard egg development enough that the first larvae are probably not present until early March. In 1975, green eggs (near eclosion) were found on 1 March, indicating first larval appearance as early March. Egg-laying may continue until September with larvae present into November. After September, development would again be prolonged due to dropping temperatures. Though red adults are probably found through December, partially black ones were found into May of the following years. As one proceeds northward, the period during the year when juvenile forms can be found becomes shorter. In Florida, juveniles are present from February through early December, whereas in North Carolina the juveniles occur commonly from May through September (Fig. 4 A) (Gray, 1946). A female lays eggs in pairs, 2 to 4 eggs every 24 hours during 2 or more weeks (Gray, 1946).

Migration and colonization of _O. disjunctus_ in northern Florida were studied by the method detailed on p. 19. Of the 10 beetles collected outside logs, 9 were discovered from 1 May to 31 October. The number of adults found in new colonies is shown for each month in Fig. 4 C. The only month in which no colonization occurred was February. Most new colonies were found in summer and fall; colonizations during the winter were preceded by several days of unseasonably warm weather. The cold season apparently causes periodicity in the life cycle of _O. disjunctus_ with regard

Fig. 4. *Odontotaenius disjunctus*. Time of year of life stages and colonization. (a) North Carolina data are from Gray (1946) and refer to the "most favorable collecting times." (b & c) Northern Florida. (b) Clear bars indicate actual field record from October 1972 to March 1975. Hatching indicates probable occurrence of a particular stage based on field observations of other stages and laboratory studies of development time. (c) The number of adults colonizing is an average for each month based on 2 years observation (October 1972-1974) of 10 logs.


A.
North Carolina
Red Adults
Pupae
Prepupae
Instar III
Instar II
Instar I
Eggs
B.
Florida
Red Adults
Pupae
Prepupae
Instar III
Instar II
Instar I
Eggs
C.
Florida
Average number of beetles per 10 logs
15
10
5
J
F
M
A
M
J
J
A
S
O
N
D
Time (months)

to both the presence of immature stages and the activities of migration and colonization.

In the mountains near Monterrey, Mexico, about 25° N. latitude, I collected passalids in late December during the cold season. Winter days are mild, but nights sometimes have temperatures below freezing. The summer is hot and has most of the precipitation. This area appears to be about the farthest north that tropical species of passalids occur in eastern Mexico. Here I found a species of _Heliscus_ and a species of _Petrejoides_ with first, second and third instar larvae present, when night temperatures were below 0°C; therefore, I suspect that in these species the life cycle is aperiodic. At the same time, however, _Odontotaenius striatopunctatus_ adults were collected there in much greater abundance, yet I found no juvenile stages. It would be particularly interesting to make a more detailed study of this area to determine if it contains some species which are aperiodic and other species which are periodic with respect to the cold season.

Lack of periodicity, or at least synchronus periodicity, of passalid life cycles is associated with a warm, moist climate and little seasonal fluctuation in temperature or rainfall in regions of Peru and Costa Rica. Life-cycle periodicity is associated with a marked dry season in southwest Costa Rica, and with a marked cold season in the United States. Both periodic and aperiodic species were found by Ohaus (1909) near Petropolis, Brazil, where the periodism was related to precipitation. Periodic and aperiodic species may inhabit the Sierra Madre Oriental near Monterrey, Mexico, an area with a definite cold season but at the northern extreme of the range of tropical passalids. In most cases, the imago was the only stage present during times of seasonal environmental stress.

ACOUSTICAL SIGNALS AND BEHAVIOR

Apparently all species of Passalidae produce sounds. Until the work of Schuster and Schuster (1971), the only modern analyses of their sounds were those of Baker (1971) for 3 African species, and Alexander, Moore, and Woodruff (1963) for _Odontotaenius disjunctus_. In the latter 2 papers, a total of 3 structurally different sound types produced by adults in 2 contexts were described. Baker described 2 kinds of disturbance signals and Alexander et al. described an aggressive signal.* Mullen and Hunter (1973) described aggressive behavior in _O. disjunctus_. Schuster and Schuster (1971) worked with 9 species of New World passalids and described 4 new acoustical signals. This study is a continuation of their work. The extent of signals now known is illustrated by the fact that in just one species, _O. disjunctus_, I describe 14 different signals associated with a minimum of 11 behavioral contexts, to my knowledge the most known for any arthropod species. This figure does not include sounds that the larvae produce. Larvae produce at least 1 sound type in a minimum of 3 behavioral contexts.

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*_Sound type_ in this paper will refer to the structure of the sound; _signal_ will refer to a particular sound type produced in a particular behavioral context.

The insect sounds familiar to most people are calling signals. Passalids lack an acoustical calling signal such as those produced by cicadas and many Orthoptera. The adult acoustical signals may be arranged into 4 general categories: (1) mating sequence, (2) aggression, (3) disturbance, and (4) other solo, i.e., signals produced in other contexts when not contacting other individuals. The larvae produce sounds (1) when disturbed, (2) when contacting adults or other larvae, and (3) when mouthing wood or frass.

Mechanisms of Sound Production

The adult's method of sound production is the subject of a controversy recently summarized by Baker (1967). One method, that of brushing cone-bearing, abdominal, epipleural plates against bristles under the elytra, was suggested by Ohaus (1900) for South American passalids and by Baker (1967) for the African genus *Pentalobus*. Another method, that of rubbing 2 spinose ovate areas on the fifth (actually the sixth according to Reyes-Castillo, 1970) abdominal tergite against the wings, was indicated in experiments with *Odontotaenius disjunctus* (Babb, 1901)

I removed the right elytron and wing of an *O. disjunctus* individual. Under a stereomicroscope, I was able to observe the left ovate area of the sixth tergite rise, move forward, and rub against the wing as the abdomen was lifted. Sound was produced with each lift of the abdomen. The return movements were silent. With a pair of fine forceps, I moved the wing slightly to one side so that the ovate area rubbed on a different part of the wing but elytral-pleural contact remained unchanged. No sound was produced, thus confirming Babb's hypothesis. In further confirmation of this, I placed a piece of paper between the wings and the tergites of individuals of O. disjunctus and Passalus affinis. This prevented Babb's mechanism from functioning but left elytral-pleural contact. Only faint noises were heard, sounding like the tergite rubbing against the paper. The reverse experiment, with paper blocking the elytral-pleural junction and the tergal-wing contact free, resulted in loud sound production. In another experiment, Reyes-Castillo and I removed the posterior-lateral portions of the elytra from an individual of Proculejus brevis. Sound was subsequently produced. These experiments lead me to conclude that, at least in New World Passalidae, sound is produced only by the tergal-wing mechanism. The importance of the wings in stridulation is emphasized by the fact that in some species, the wings are so reduced that they are incapable of flight, yet they retain the stridulatory mechanism as an enlarged distal area at the end of a long, thin strap (Arrow, 1904).

Baker (1967) repeated one of Babb's experiments using Pentalobus. He removed the wings above the wing fold, but found that the beetles were still able to stridulate. He states that the spiny ovate areas on the sixth abdominal tergite and ridges on the wing fold are not as well developed in Pentalobus as in O. disjunctus and attributes stridulation to the elytral-pleural mechanism. When I removed the wings of O. disjunctus no sounds were subsequently produced, but when the wings were removed from P. brevis faint sounds were heard, seemingly the ovate areas rubbing against the elytra. Perhaps this sound is what Baker heard as well.

The larvae also stridulate. The mechanism appears to be the same for all species. Riley (1872) and Sharp (1901) described the stridulatory apparatus. The metathoracic legs are reduced, forming specialized structures that rub against striated areas on the mesothoracic coxae.

Ritcher (1966) mentions that the dorsal surface of the stipes of passalid larvae have conical stridulatory teeth. I have never heard sounds that I could attribute to maxillary stridulation, nor does he mention any.

Frequency Analysis

Since the U.S.D.A. Agricultural Research Service's Insect Attractants, Behavior and Basic Biology Laboratory (IABB Laboratory) in Gainesville, Florida, was kind enough to offer me an opportunity to use their well equipped sound laboratory, I was able to do frequency analyses, as well as a few other tests on some representative passalids. In some insects which have broad spectrum, buzz-like sounds similar to Passalidae, such as Tettigoniidae, much of the sound energy is actually in the ultrasonic frequencies.

Frequency analyses were made of the disturbance signals of 2 beetles each of _Passalus affinis_, _P. punctatostriatus_, and _Odontotaenius disjunctus_. The beetles were placed less than 2 cm from a microphone (either a Bruel and Kjaer condenser 1/2-inch type no. 4133, or a Bruel and Kjaer condenser 1/2-inch type no. 4135) in a specially constructed anechoic chamber at the U.S.D.A., IABB Laboratory. Sounds were elicited by squeezing or blowing upon the beetles. The sound was fed into a Honeywell 5600 Magnetic Tape Recorder (frequency response ±3 db at 15 inches per second, 100-75,000 Hz; at 30 i.p.s., 150-150,000 Hz) using 1/2-inch Ampex Instrumentation Tape. The signal was then passed via a McIntosh Power Amplifier Model MC75 to a Signal Analysis Industries Corp. SAI-52 Real Time Spectrum Analyzer-Digital Integrator. The resulting analysis was printed up to 80,000 Hz by a Honeywell 540 XYY' Graph Recorder. Control analyses were run on the anechoic chamber without the beetles as well as the tape by itself without the microphone.

Results

The controls as well as the test analyses showed high peaks below 2,000 Hz (highest peaks below 500 Hz), apparently due to circuit "noise" and tape "hiss." The sounds of the 3 species were all quite similar with most energy peaking in the range from 4,000 to 10,000 Hz (Fig. 5). Individuals of all 3 species produced detectable sounds up to 16,000 Hz. These tests suggest that passalid signals contain no significant energy at ultrasonic frequencies.

Sound Pressure Level Analysis

Materials and Methods

Sound pressure levels were compared among the same 3 species at the U.S.D.A. IABB Laboratory. The same microphones and procedures were used as in the frequency analyses. The subsequent sound produced was fed directly into a 2608 Bruel and Kjaer Measuring Amplifier for pressure level determination.

Results

Sound pressure levels for 4 individuals are given in Table 2. The levels for beetles of the smaller species were lower than those of the larger species. This confirms my casual observations that larger beetles generally made louder disturbance signals.

Sound Structures, Behavioral Contexts, and Species Repertoire

Materials and Methods

Logs were carefully dissected in the field to determine which passalids were found in the same tunnel system. Each such group was caged separately in a terrarium or in

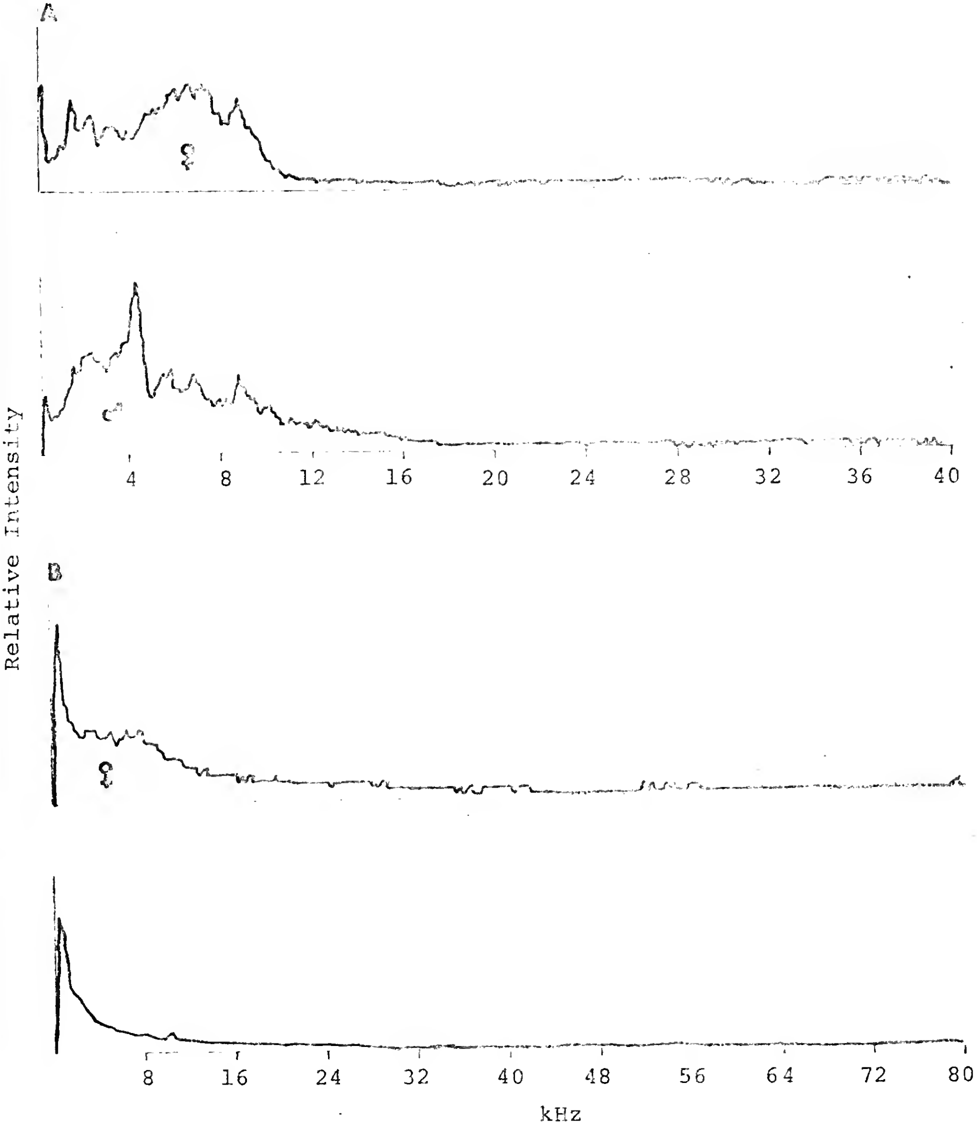

Fig. 5. Representative frequency analyses of disturbance signals of Passalidae. (a) Frequency analyses of ♀ and ♂ *Passalus affinis*. (b) Frequency analyses of *Odontotaenius disjunctus* and control without beetle--due to scale differences (a) is not directly comparable to (b) on either axis.

Table 2. Comparison of sound pressure levels (S.P.L.) and body length of 4 individuals of 3 species of Passalidae. S.P.L. were measured using 1/2 inch and 1/4 inch condenser microphones at 76°F.

Species	Body length (mm)	S.P.L. (dB)* 1/2" mic	S.P.L. (dB)* 1/4" mic
Passalus affinis	43	--	67.4
Odontotaenius disjunctus	38	66	65.4
Passalus punctatostriatus	23	49	--
Passalus punctatostriatus	24	46	--

*re: 2×10^{-5} N/m^2.

a large (15 cm x 2 cm) petri dish. These were kept in my home in places which would maximize observation time (e.g., kitchen table). One method effective in stimulating sound production was introducing other passalids that had been isolated for a week or more.

Sounds of beetles from Peru, Ecuador, Colombia, Panama, Puerto Rico, Belize, and central Mexico (i.e., states of Hidalgo, Puebla, and Veracruz) were recorded at 3 3/4 i.p.s. on a Craig 212 battery-operated portable tape recorder with a Craig microphone. To check for variation in tape speed, time markers (i.e., a single sharp sound every 5 sec for over a minute) were recorded on several tapes when new batteries were inserted into the recorder. The recorder's speed was checked using the time-marked tapes before recording and before making audiospectrographs. Variation in tape speed was less than 5%. By using a note from a banjo, it was possible to check for wow and flutter. Beetles from Costa Rica and Jamaica were recorded on a Roberts 720 stereo tape recorder at 7 1/2 i.p.s. with a Roberts Model 3815 microphone. Those from the United States, the Dominican Republic, and northern Mexico (i.e., states of Tamaulipas and Nuevo León) were recorded at 7 1/2 or 15 i.p.s. on a Kudelski Nagra III tape recorder with an American D33A microphone. Temperatures were measured in all cases with the same calibrated thermometer. The first 2 tape recorders and an Ampex Model 351 were used for playback analysis. Audiospectrograms were made with a Kay Electric Co. Sonagraph audiospectrograph. Sounds were played into the Sonagraph at original tape speed. The Sonagraph voltage unit meter was kept at a level of -5 or below.

Field monitoring of occupied logs in the United States was with a Sonitrol Corp. Sonitrol Detector and with the Nagra III tape recorder with the American D33A microphone placed against the wood. The tape recorder detected sounds as well as, if not better than, the Sonitrol. In the Dominican Republic, a Kudelski Nagra IV tape recorder with an American D33A microphone was used. Logs chosen for field studies were small (7 1/2 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. This was determined in separate observations by use of a Bailey Instrument Co. BAT-4 Thermocouple indicator and 3 thermocouple probes.

Results

Acoustical signals were recorded from 42 species of Passalidae (Tables 3 and 4). They are produced in a variety of behavioral situations, as outlined at the top of the tables. These signals may be classified on the basis of the structure of the sound into 7 types, A-G. Which of these types are produced by any given species in particular situations is indicated in the body of the table.

Sound structure

Passalid sounds may be described in terms of "pulses," "bars," and "phonatomes." The first 2 terms depend only on sound structure, whereas the latter requires knowledge of how the sound is produced. A pulse is "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.* A series

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*The term pulse in Schuster and Schuster (1971) is here replaced by the term bar.

Table 3. Types of disturbance signals recorded or heard from individuals of 42 species of New World Passalidae from 11 countries.

Species	Collecting locality	# of individuals studied	Sound types during disturbance
PROCULINI			
Heliscus tropicus (Percheron)	Mexico-central	4	A
Heliscus sp. n.	Mexico-northern	7	A
Odontotaenius zodiacus (Truqui)	Mexico-central	9	A (C)[1]
O. disjunctus (Illiger)	U.S.-Florida, Mich.	150	A
O. striatopunctatus (Percheron)	Mexico-northern	15	A (B)
	Mexico-central	4	A B
	Belize	5	A B
Spurius sp.	Mexico-central	1	A
Oileus rimator (Truqui)	Mexico-central	8	A
O. nonstriatus (Dibb)	Mexico-central	2	A/C
Petrejoides sp. n.	Mexico-northern	5	A (C)
Proculejus brevis Kaup	Mexico-central	4	- B
Verres corticicola (Truqui)	Mexico-central	6	A
V. hageni Kaup	Costa Rica	4	A
	Panama Canal Zone	4	A
Veturius platyrhinus (Westwood)	Peru	60	A
	Colombia	10	A
V. cf. bolivae (Gravely)	Peru	5	A
Vindex agnoscendus (Percheron)	Mexico-central	1	A
PASSALINI			
Spasalus sp. IXB	Peru*	7	A
S. crenatus (Mac Leay)	Peru	3	A (C)
	Puerto Rico	8	A
Paxillus leachi Mac Leay	Peru	2	A

Table 3 (continued)

Species	Collecting locality	# of individuals studied	Sound types during disturbance
Paxillus sp.	Peru	2	A
Ptichopus angulatus (Percheron)	Mexico-central	3	A
Passalus (Pertinax) affinis Percheron	Dominican Rep.	23	A
P. (P.) caelatus Erichson	Peru	7	A(C)(F)
	Colombia	4	A
P. (P.) convexus Dalman	Peru	45	A
P. (P.) dominicanus Van Doesburg	Dominican Rep.	8	A
P. (P.) inops Truqui	Mexico-central	1	A/C B
P. (P.) punctatostriatus (Perch.)	Mexico-northern	5	A B
	Mexico-central	1	A
	Belize	2	A
P. (P.) morio Percheron	Peru	20	A
P. (P.) nr. caelatus	Peru	3	A
P. (P.) sp. n.	Ecuador	5	A
P. (Mitorhinus) spinifer Perch.	Peru*	10	A B
P. (Passalus) sp. VIII	Peru	2	A
P. (P.) sp. XV	Peru	4	A B(C)
P. (P.) nr. toriferus Esch.	Peru	3	A
P. (P.) jansoni (Bates)	Costa Rica	1	A
P. (P.) pugionifer (Kuwert)	Peru	10	A
P. (P.) elfriedae Luederwaldt	Peru	10	A
P. (P.) nr. elfriedae	Peru	3	A
P. (P.) sp. IVB	Peru	10	A

Table 3 (continued)

Species	Collecting locality	# of individuals studied	Sound types during disturbance
P. (P.) coniferus Eschscholtz	Peru	50	A
P. (P.) interruptus L.	Peru	55	A
P. (P.) interstitialis Esch.	Peru	30	A B
	Panama Canal Zone	1	A B
	Jamaica	5	A B
P. (P.) punctiger Lepeletier et Serville	Peru	60	A
	Colombia	10	A
	Panama Canal Zone	1	A
	Costa Rica	6	A
	Belize	2	A
	Mexico-northern	10	A

[1] All sound types in parentheses are rare.

*First record from this country.

Table 4. Types of sounds observed in 10 behavioral contexts other than disturbance from 24 species of Passalidae.

Species	Courtship initiation	Courtship ♂	Courtship ♀	Post-copulation	Strong agg.: Aggressor	Aggressor	Aggressee	Mild aggression	Post-agg. pushups	Other solo
PROCULINI										
Proculejus brevis					C			E		
Petrejoides sp. n.	C	A			C	B				
Heliscus sp. n.					C					
Oileus rimator					C	B				
Odontotaenius zodiacus	C	-	A	CB	C	C				
O. striatopunctatus (N. Mex.)	-	-	-		CE	B(C)^1		D		
O. disjunctus	C	A	A	ADE	CE	BE	A	D		D(B)
Verres hageni (Costa Rica)					C			D		
Veturius platyrhinus (Peru)								(D)		
PASSALINI										
Spasalus crenatus (Peru)					C					
Passalus (Pertinax) affinis	C	A		A	CE	BE	A			
P. (P.) caelatus (Peru)	C	A								
P. (P.) convexus	C	A	A			B		A	F	E
P. (P.) dominicanus							A			(B)
P. (P.) inops										(B)
P. (P.) punctatostriatus (N. Mex.)	C	A	A		C	B				

Table 4 (continued)

Species	Courtship initiation	Courtship ♂	Courtship ♀	Post-copulation	Strong agg.: Aggressor	Aggressor	Aggressee	Mild aggression	Post-agg. pushups	Other solo
P. (Mitorhinus) spinifer	C	A								E
P. (Passalus) near toriferus	C	A			E*	E*				
P. (P.) jansoni						E*				
P. (P.) elfriedae	C	A			C					
P. (P.) coniferus	C	A	A		C					
P. (P.) interruptus	C	A			C	E*				
P. (P.) interstitialis (Peru)						(E)				
P. (P.) punctiger (Peru)	C	A	A		C					
(Costa Rica)	C	A	A		C(B)			E		
(N. Mexico)	C	A	A	A	E			D		GD

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[1] All sound types in parentheses are rare.

[*] Only in interspecific interactions.

of bars produced at a constant rate with bars of about equal duration forms a *simple bar train*; at a varying rate and/or with bars of unequal duration, a *complex bar train*. 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 the case of adult Passalidae).

The 7 types of sounds produced by adult passalids are described in the following key.

Key to Adult Passalid Sounds (26°C)

Bars longer than 0.06 sec; phonatome consists of 1 bar (Fig. 6) . . . . TYPE A

Bars shorter than 0.06 sec; phonatome consists of 1 or more bars.

- Complete sequence of sounds consists of 1 bar, or a series of bars produced in an irregular pattern (Fig. 9) . . . . TYPE D
- Complete sequence of sounds consists of a series of bars produced in a regular pattern (Figs. 7, 8, 10, 11, 12)
  - 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 (Fig. 11) . . . . TYPE F
  - Sequence composed principally of unpaired units, occasional paired units not as above.
    - Phonatome consists of 1 bar; sequence a simple bar train (Fig 7) . . . . TYPE B
    - Phonatome consists of more than 1 bar; sequence a complex bar train.

Eighty percent of more of bars longer than 0.01 sec (Fig 8) . . . . TYPE C

Eighty percent or more of bars shorter than 0.01 sec.

End of phonatome with 2 or more bars longer than 0.01 sec (Fig. 12) . . . . TYPE G

End of phonatome with at most 1 bar longer than 0.01 sec (Fig. 10) . . . . TYPE E

Whereas a bar of most sound types has a more or less "rasping" texture, those of Type F sound more like "clicks" or "snaps." The behavior of the beetle is quite peculiar during the production of this sound. The pair of clicks is produced as the beetle partially straightens the hind legs so that the posterior portion of the body is briefly raised, as if it were doing a "pushup" with the hind legs.

The fine structure of representative sounds was analyzed on an oscillograph (Honeywell 2160 Visicorder). It was discovered that sound units which were superfically similar (the <u>bars</u> defined above) could consist of either a pulse or a train of closely spaced pulses. For example, even in a single sequence by 1 individual the bar comprising a Type A phonatome sometimes consists of a pulse, sometimes of a pulse train. Also, 1 of the bars of a Type C phonatome may consist of a single pulse (Fig. 13 A) or a pulse train (Fig. 13 C).

Larval sounds are fundamentally different from those of the adult in that a sound may be produced on both the

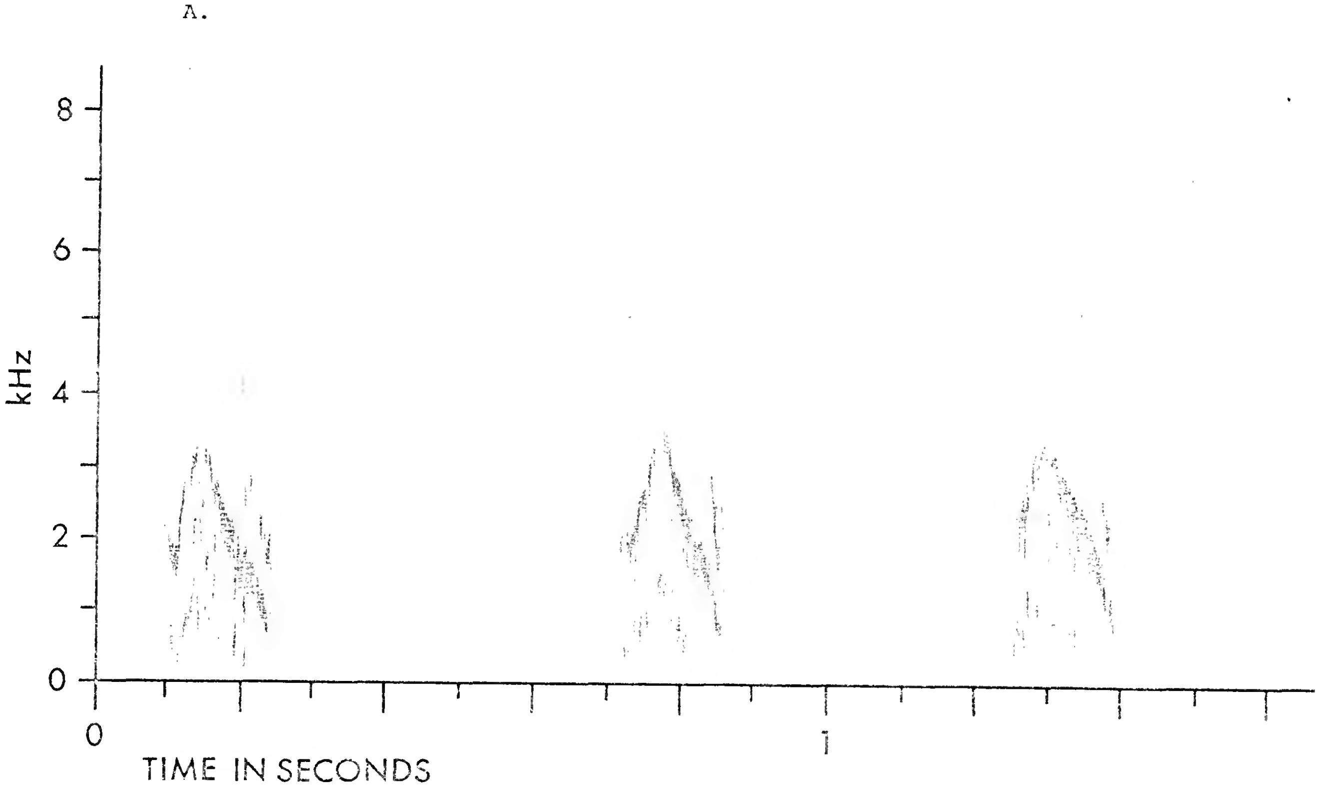

Fig. 6. Audiospectrograms of Type A sounds. (A) Disturbance signal of *Passalus* near *toriferus*, 25°C.

B.

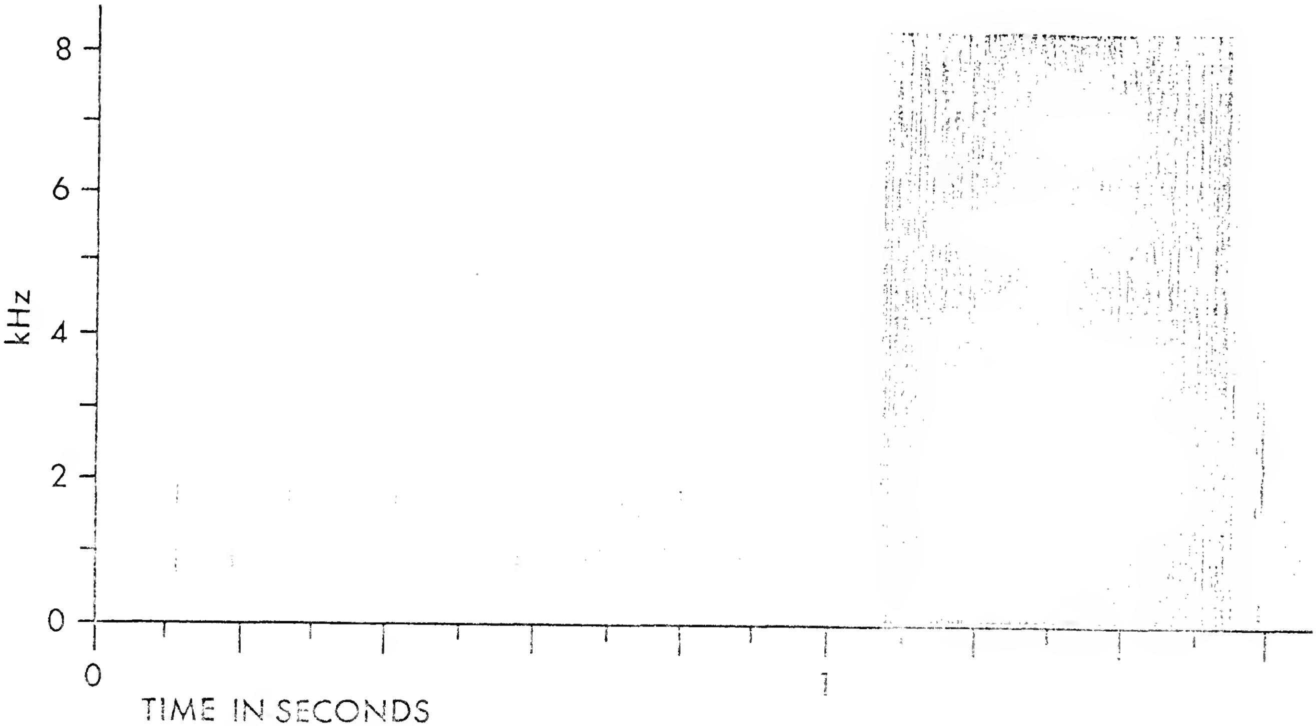

Fig. 6 continued. (B) Post-copulation signal of *Passalus affinis* 24.5°C.

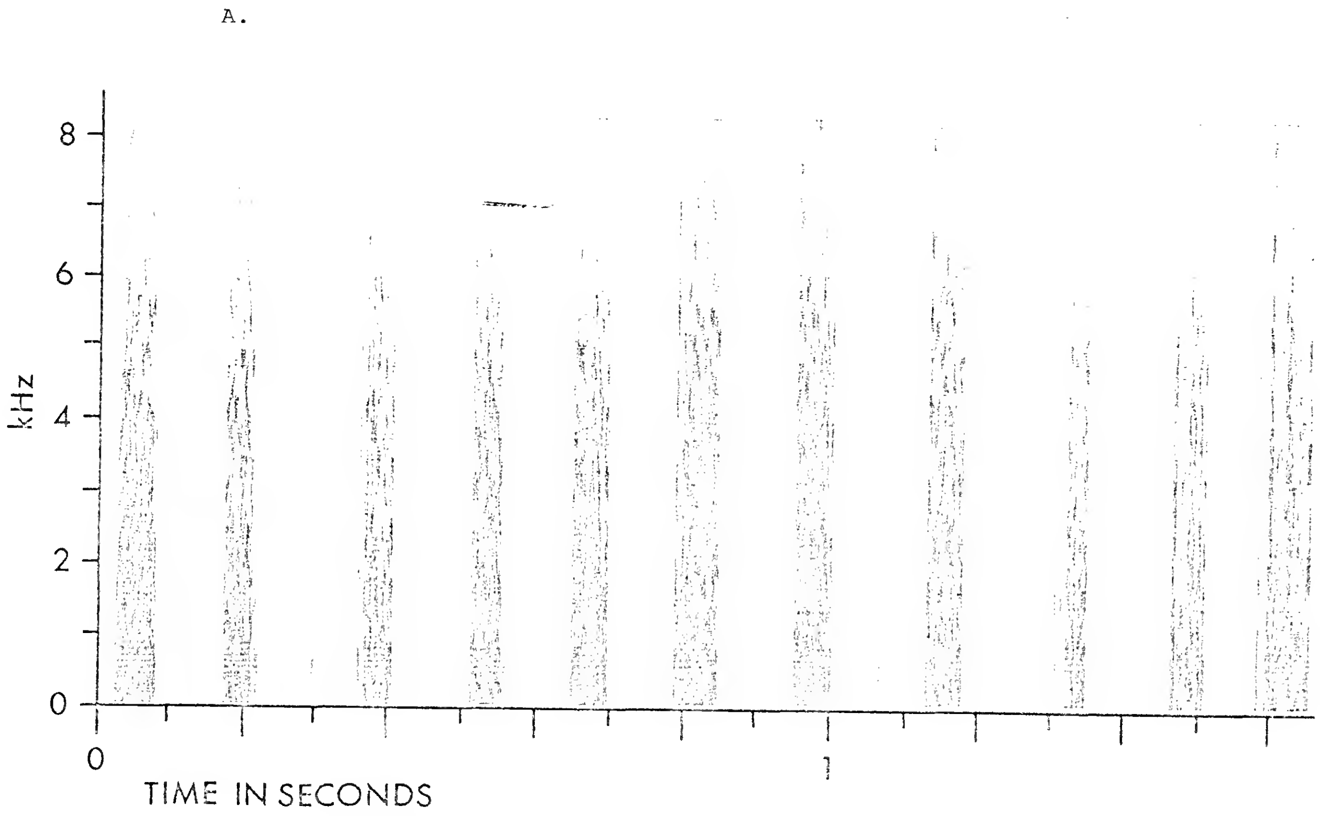

Fig. 7. Audiospectrograms of Type B sounds. (A) Female aggressive signal of *Passalus convexus*, 26.5°C.

B.

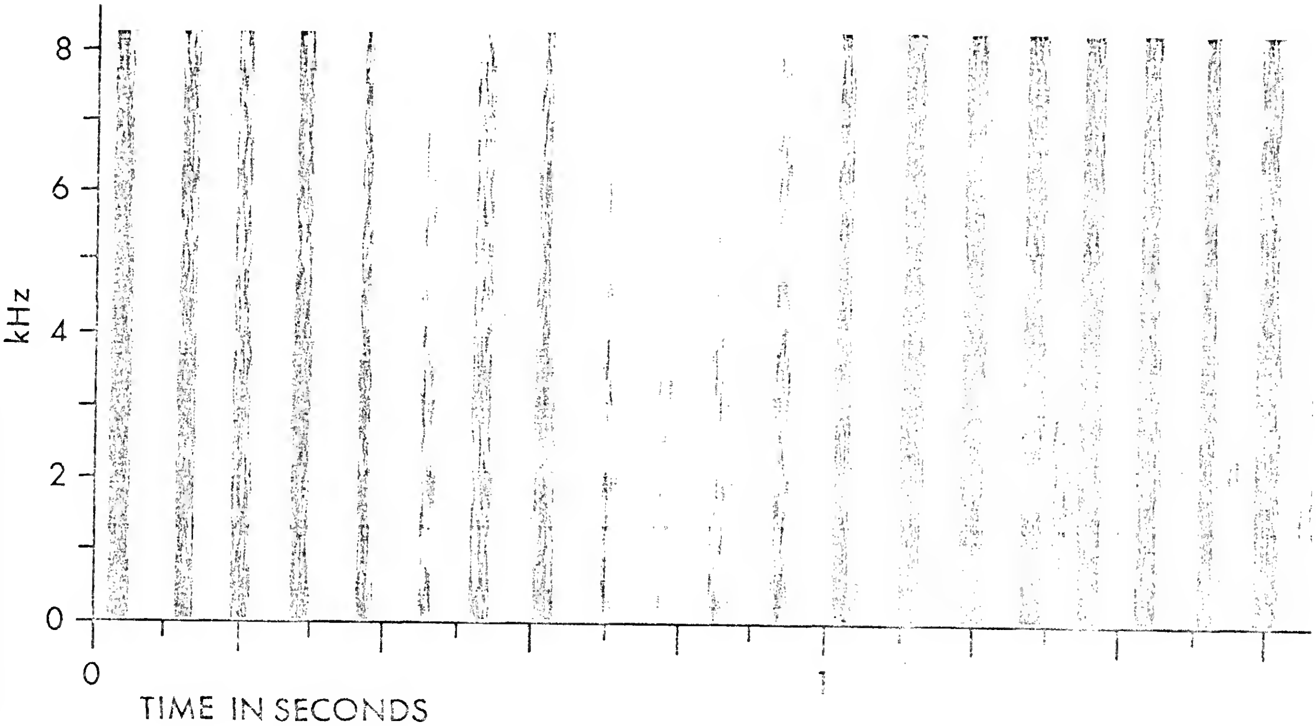

Fig. 7 continued. (B) Female aggressive signal of *Odontotaenius striatopunctatus*, 28°C.

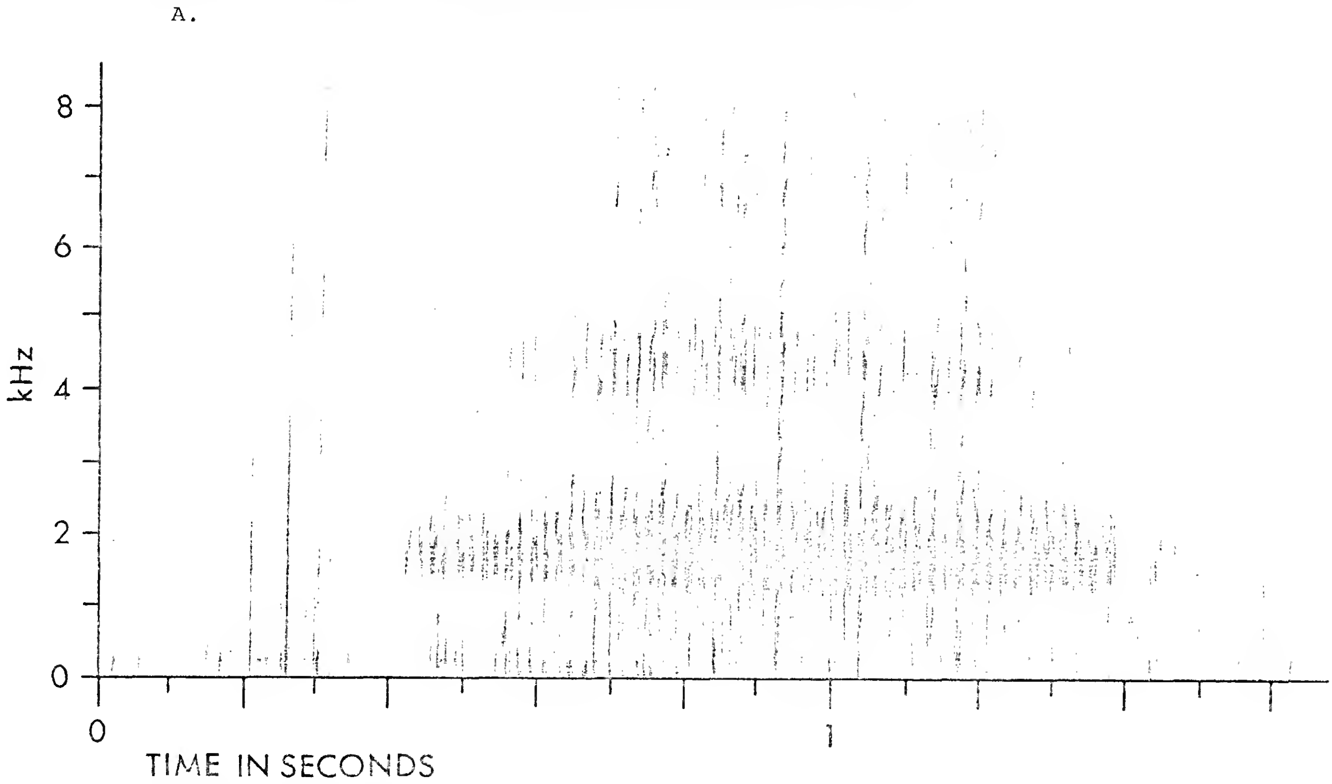

Fig. 8. Audiospectrograms of Type C sounds. (A) Courtship initiation signal of *Odontotaenius zodiacus*, 24°C.

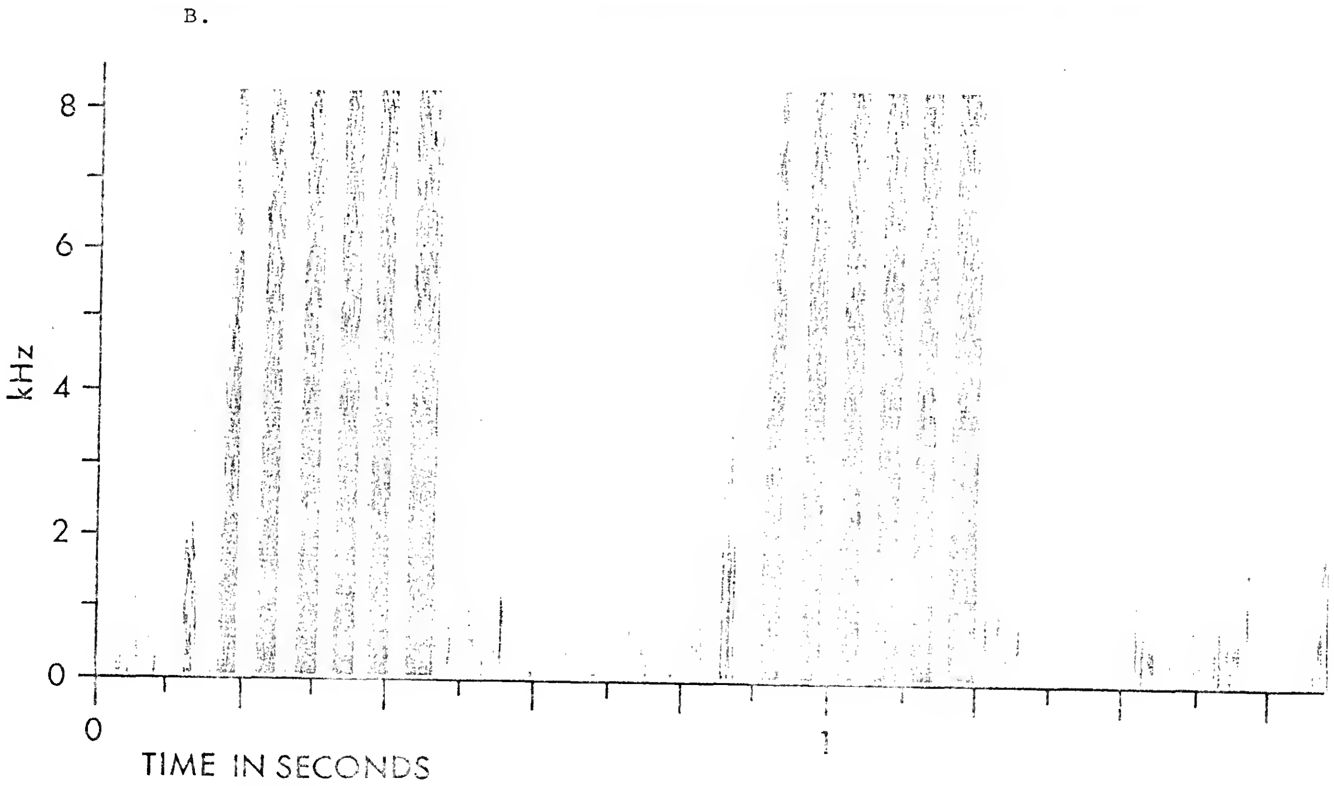

Fig. 8 continued. (B) Courtship initiation signal of Passalus convexus, 26.5°C.

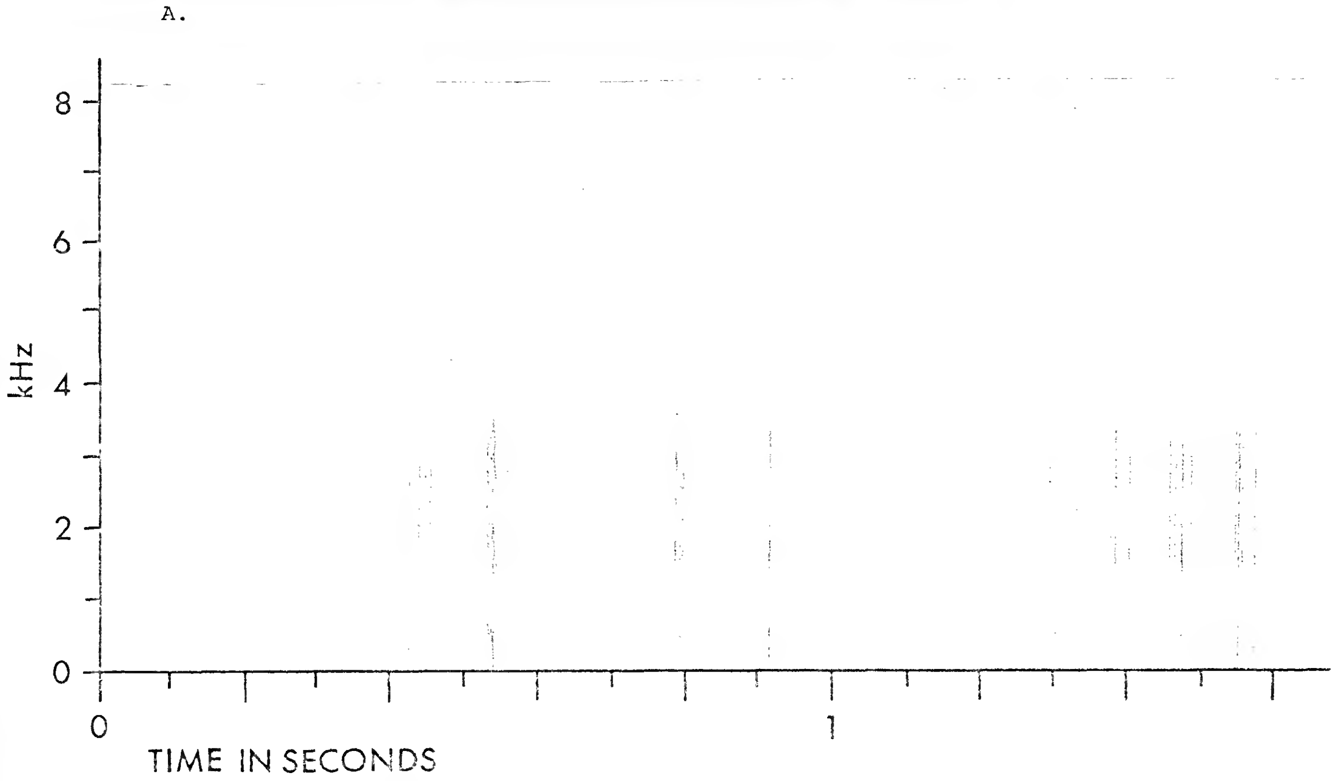

Fig. 9. Audiospectrogram of Type D sounds. (A) Mild aggression signal of *Passalus punctiger*, 30°C.

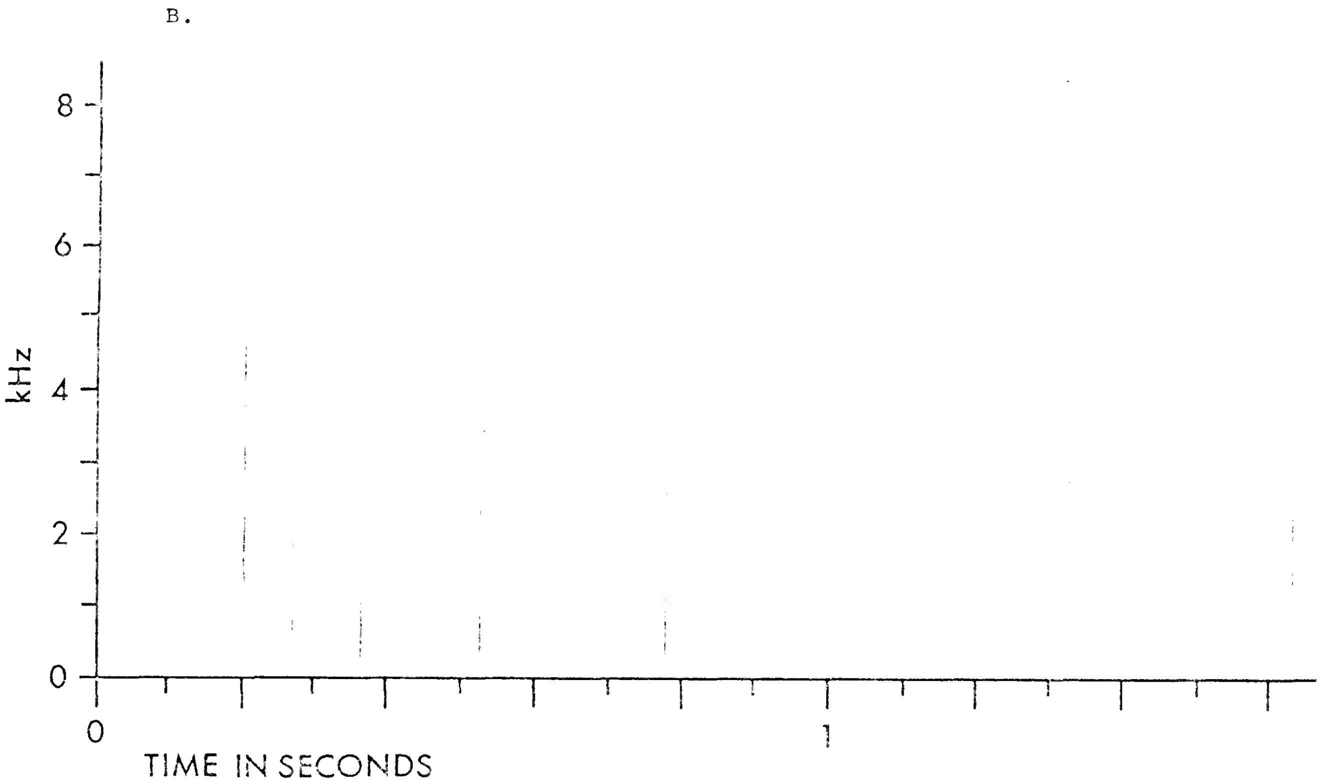

Fig. 9 continued. (B) Signal produced in field log by *Odontotaenius disjunctus*, 30°C.

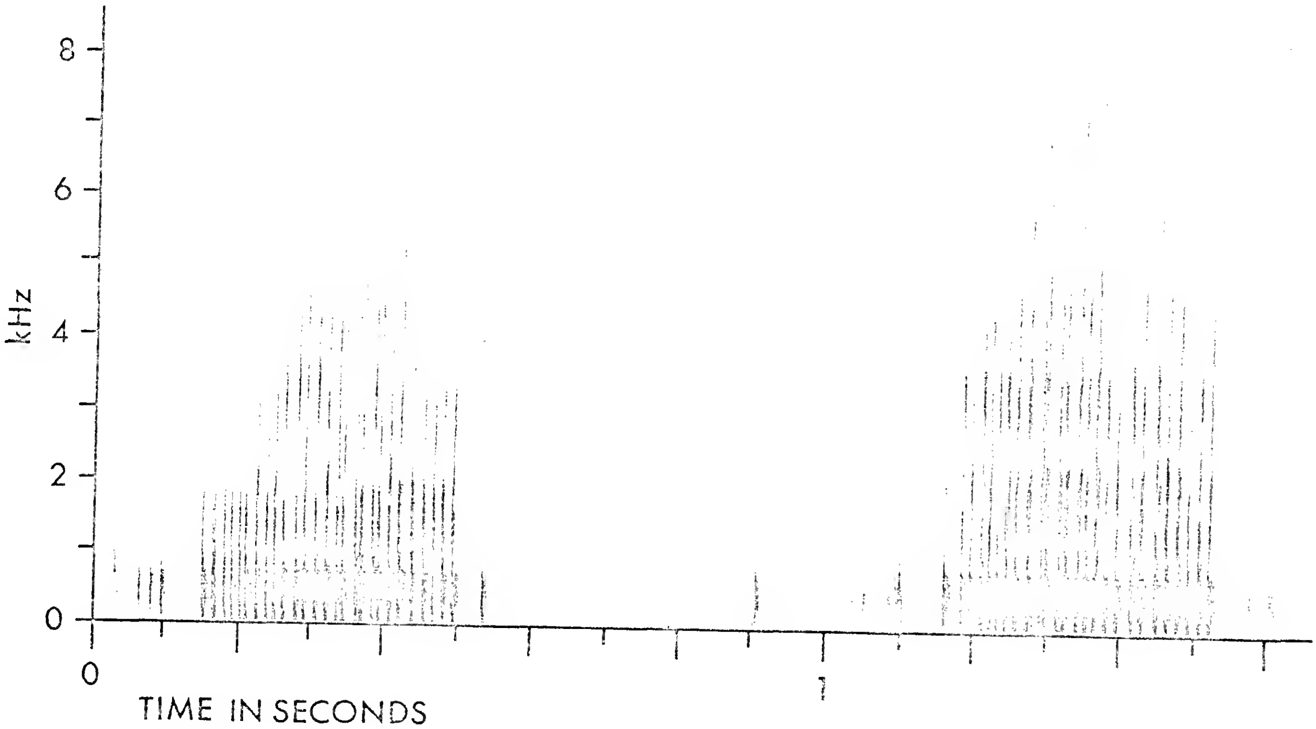

Fig. 10. Audiospectrogram of Type E sounds; signal produced while alone by <u>Passalus spinifer</u>, 26.5°C.

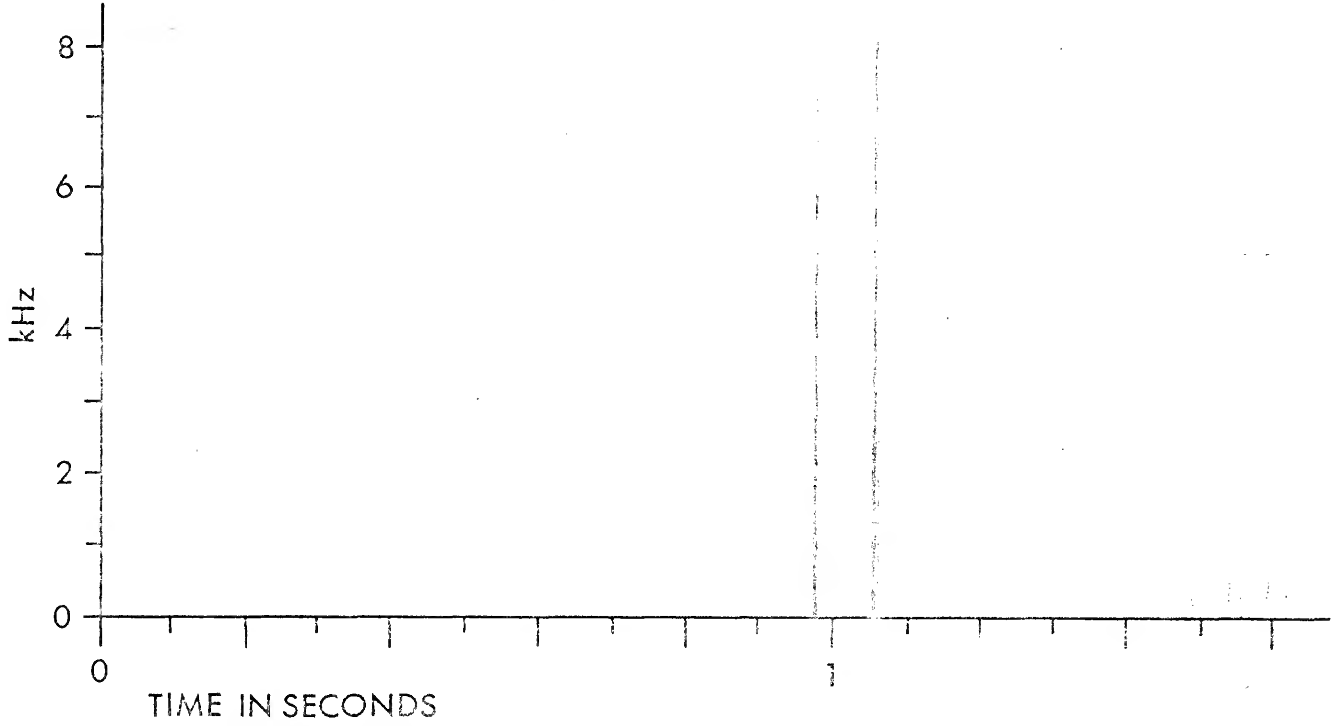

Fig. 11. Audiospectrogram of Type F sound produced during post-aggression pushups by Passalus convexus, 25.5°C.

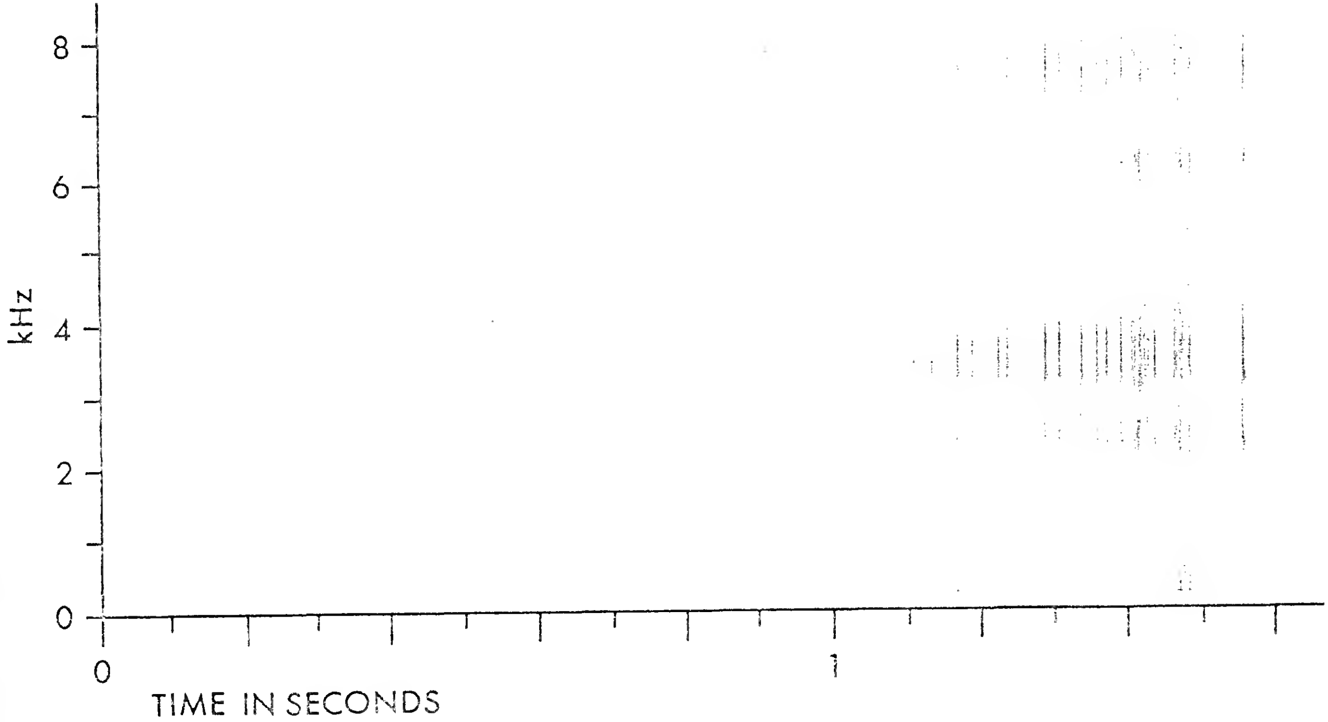

Fig. 12. Audiospectrograms of Type G sounds produced while feeding by *Passalus punctiger*, 28°C.

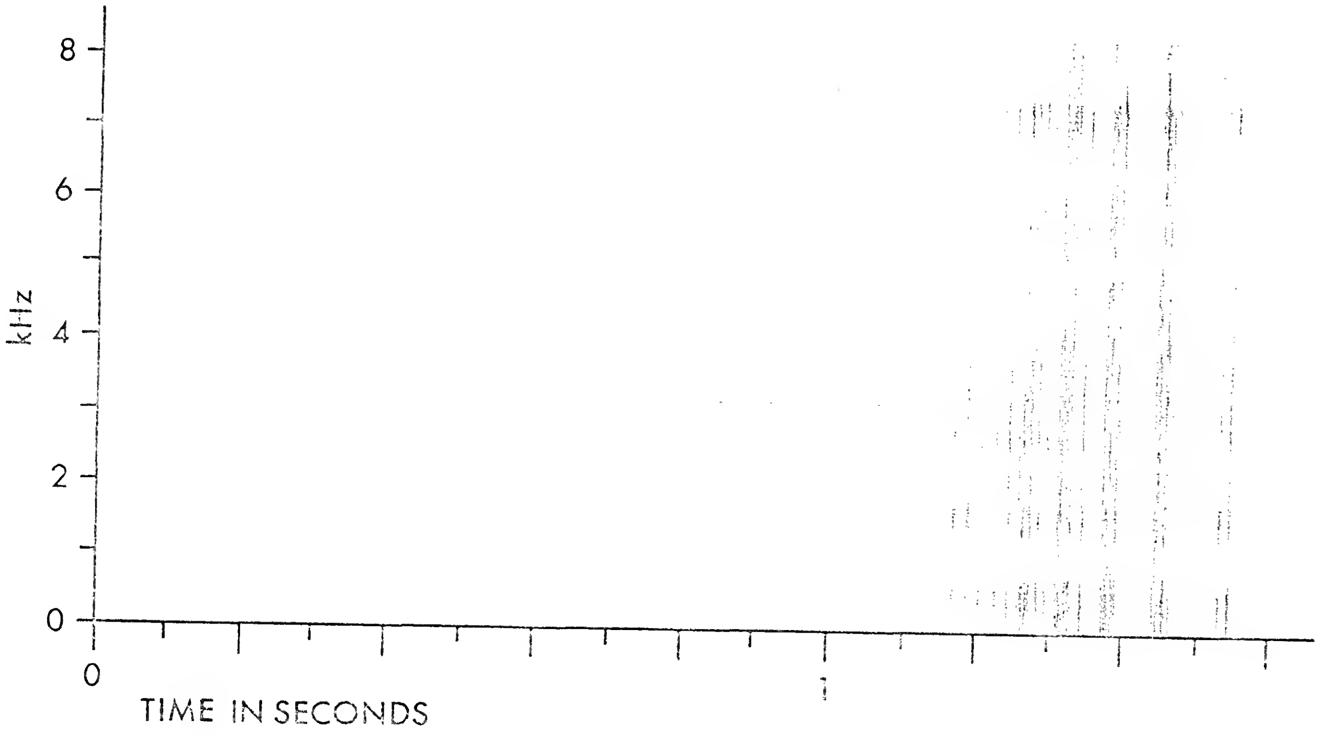

Fig. 12 continued.

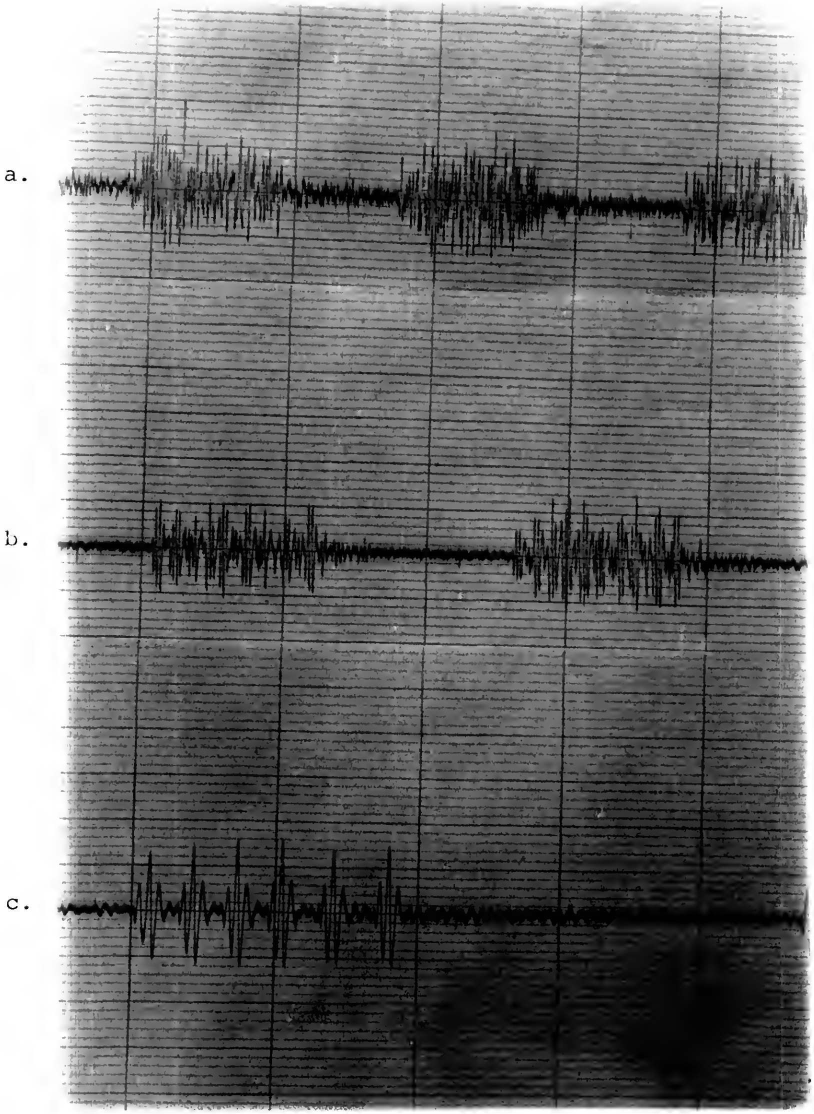

Fig. 13. Oscillograms of bars of Type C phonatomes of 3 species of Passalidae. (a) *Odontotaenius disjunctus*, (b) *Passalus affinis*, (c) *Passalus* sp. XV.

upstroke and the downstroke of the stridulatory apparatus (Fig. 14). By manually rubbing a metathoracic leg against the coxal striae, I produced the loudest sound on the downstroke with larvae of Odontoaenius disjunctus and Pharochilus politus. Sounds are most similar structurally to the Type A or Type B sounds produced by the adults.

Behavioral contexts and species comparison

The types of sounds described above are produced in a number of different behavioral situations. For example, the sounds produced in a disturbance situation, the "disturbance signals," are commonly of Type A, sometimes of Type B, C, or other types. The various behavioral situations are described below, along with a comparison of the signals of different species.

Mating sequence. The reproductive sequence consists of 4 stages: (1) courtship initiation, (2) courtship, (3) copulation, and (4) post-copulation. Positions of beetles and sounds frequently produced in each stage are summarized for Odontoaenius disjunctus in Fig. 15. Sounds are not usually produced during copulation and therefore this will not be treated here. Copulation was described in Schuster (1975).

Courtship initiation. Upon contacting the female with his antennae, the male produced a Type C sound, the same type as produced by a male during aggression, though usually of less

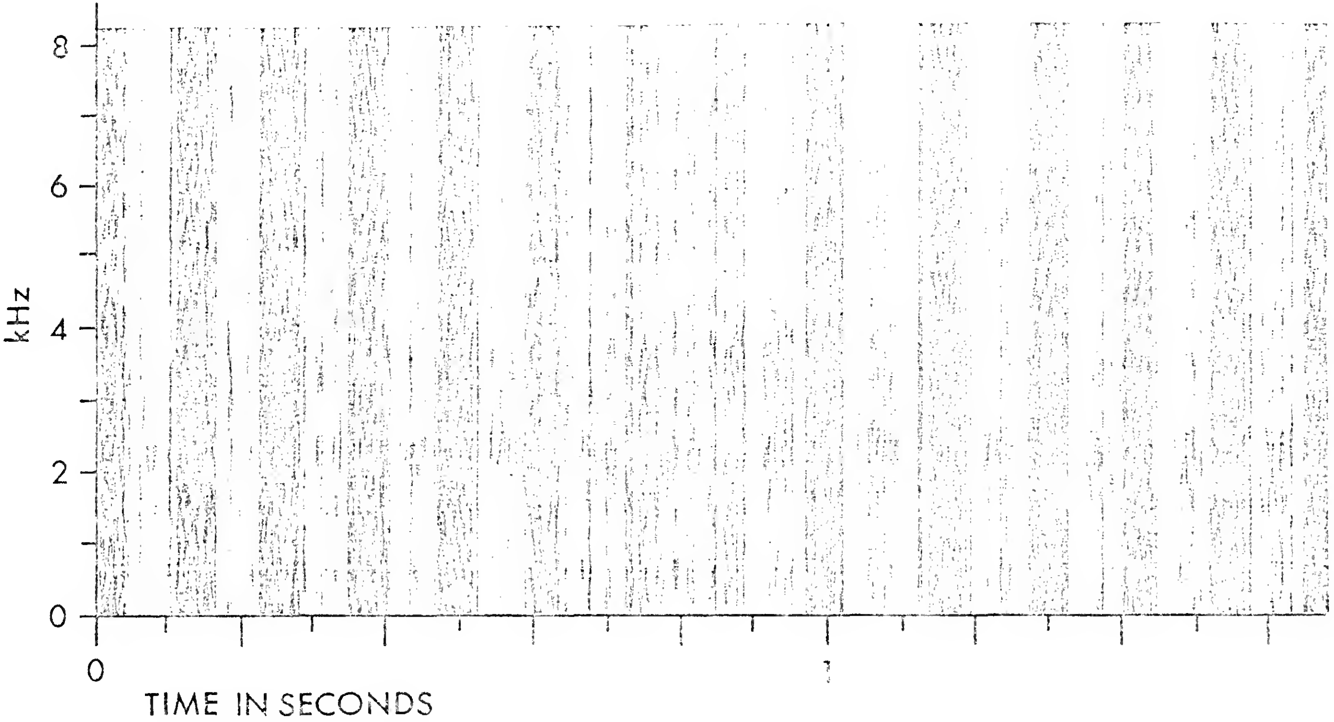

Fig. 14. Odontotaenius disjunctus--audiospectrogram of larval sounds when contacting adult, 29.5°C.

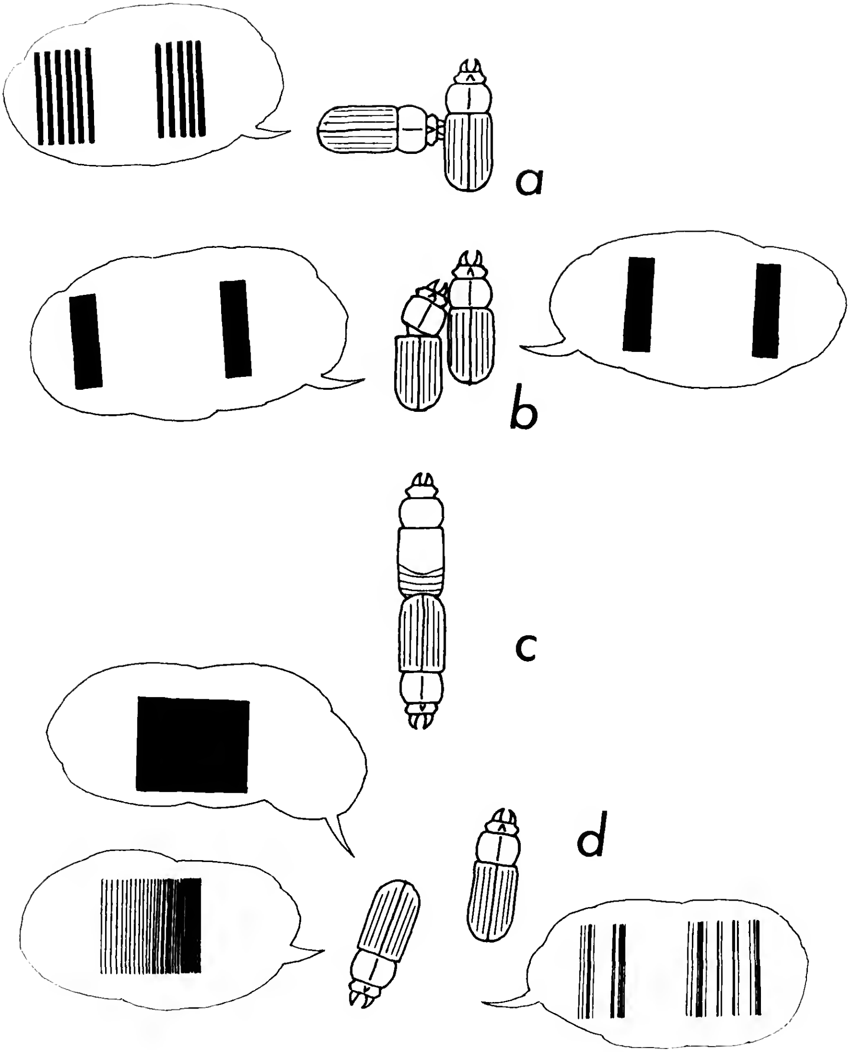

Fig. 15. Odontotaenius disjunctus -positions of beetles and sound types during the mating sequence. (a) courtship initiation, (b) courtship, (c) copulation and (d) post-copulation. The clouds contain diagrams of audiospectrograms and indicate the beetle producing the sound.

intensity. Courtship initiation is also similar to aggression, though usually of less intensity. Courtship initiation is also similar to aggression in that the male's head is to the other animal's side or rear (Fig. 15 a), but dissimilar in that the male roots the female little or not at all and she does not tilt downward the side of her body facing him. Each beetle vibrates its antennae against the body of the other but less vigorously than during aggression. The affinity between courtship initiation and aggression was further illustrated in 2 cases, 1 with _Passalus interruptus_ and the other with _P. elfriedae_, in which behavior indistinguishable from aggression initiated the sequence and was followed by courtship.

The Type C courtship initiation signal is known from 13 species; in 9 of these, Type C sounds have also been observed during aggression (Table 4). One species, _Odontoaenius zodiacus_, produced a Type C courtship initiation signal that is very different from those of the other species. Its phonatome is 0.63 to 0.97 sec long and consists of 30 to 53 very closely spaced bars (Fig. 8 A). The phonatome of all other species is shorter (less than 0.56 sec), and contains considerably fewer bars (13 or less--Fig 8 B). The number of bars/phonatome varies with the species, e.g., 2 to 4 in _Passalus punctiger_ from Peru, and 7 to 13 in _P. affinis_.

The courtship initiation signal may aid in communicating the beetle's identity as a male to the female, since Type C sounds are usually produced only by males (Table 4). The courtship signal would not serve this function because the male and female signals are similar. The courtship initiation signal may help the male to inform the female of his readiness to mate, and act as a releaser of female courting behavior.

Courtship. Courtship initiation gives way to courtship as the male switches from the Type C sound to a Type A sound. This occurs while his head is still to the female's side. Subsequently, he turns so that he is parallel to her, usually facing in the same direction, and they walk in a circle with the female on the inside (Fig. 15 b). Repeatedly, the male shifts from the parallel position to the head-to-side position and back again. In the head-to-side position, he may switch from the Type A sound to the Type C sound and vice versa; in other words, behavior similar to courtship initiation is recurrently intercalated into the courtship sequence. This "dance" comprised of courtship and courtship initiation behavior may continue for up to 12 hours, the male stridulating constantly. If separation occurs, recontact is followed by courtship initiation behavior.

The female also produces a Type A courtship signal, but less constantly than the male. When she stridulates, she usually does so in approximate one-to-one relationship with the male's phonatomes, sometimes overlapping, sometimes alternating with his (Fig. 16). In Odontotaenius disjunctus, the female courtship signal occurs only with the male courtship signal (Fig. 16), but in Passalus punctatostriatus, the male spends more time than do males of other species in the head-to-side position producing the courtship initiation signal and the female produces her courtship signal with it (Fig. 17). In Odontotaenius zodiacus, there is apparently no male courtship signal and the female courtship signal is produced alone during courtship as well as in company with the male's Type C signal during courtship initiation.

The male courtship signal, known from 12 species (Table 4) ranges from 0.06 to 0.31 sec in phonatome duration. It resembles the disturbance signal in that both are Type A sounds, but generally differs from the latter in pitch and length. The pitch remains relatively constant throughout a courtship phonatome, but varies during a disturbance phonatome. In some species, the courtship signal is shorter than the disturbance signal (e.g., in Petrejoides sp. n., courtship = 0.09 to 0.12 sec, disturbance = 0.16 to 0.35 sec at 23°C). In other species, the courtship signal is longer than the disturbance signal (e.g., in Passalus spinifer, courtship = 0.13 to .17 sec, disturbance = 0.06 to 0.10 sec at 24 1/2°C), and in some they are of similar duration. The commonest situation among species appears to be courtship signals shorter than disturbance signals. In most cases, the variation in length at a given temperature is less for courtship phonatomes than for disturbance phonatomes of the same individual (e.g., in a <u>Passalus convexus</u> male at 26°C, courtship: $\bar{x}$ = .23 sec, coefficient of variation, CV = .18; disturbance: $\bar{x}$ = .42 sec, CV = .30; n = 5 and 5). The female courtship signal, known from 5 species (Table 4), is similar in length to that of the male.

The courtship signals may aid in keeping the pair together, increase the other individual's readiness to copulate, and inform the other individual of the signaler's readiness to copulate. Recurrence of the courtship initiation signal may reinform the female of the male's sex.

In 2 species, certain signals were apparently lacking. Males of <u>Odontotaenius zodiacus</u> did not produce a courtship signal though they did produce a courtship initiation signal and the female produced courtship signals. In <u>O. striatopunctatus</u> (from northern Mexico), female and male courtship signals as well as the courtship initiation signals were lacking. The sigle pair studied performed a silent "dance" on at least 2 occasions, culminating in copulation once. In contrast, the male produced Type C sounds in aggression, and both he and the female produced Type A sounds when disturbed.

At times during the dance, the male or female may place a hind leg upon the posterior portion of the elytra of the other beetle. At other times, 1 of the pair (usually the

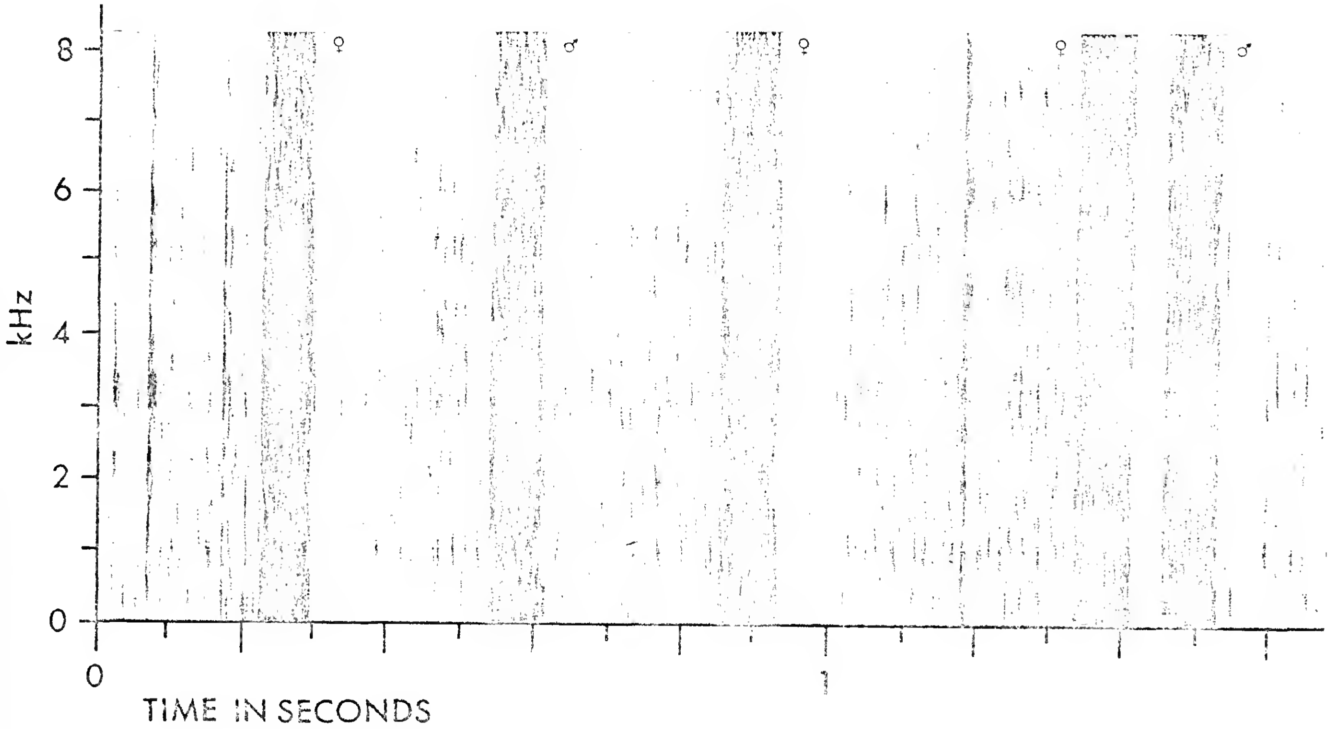

Fig. 16. Odontotaenius disjunctus--courtship, ♂ and ♀ 26°C.

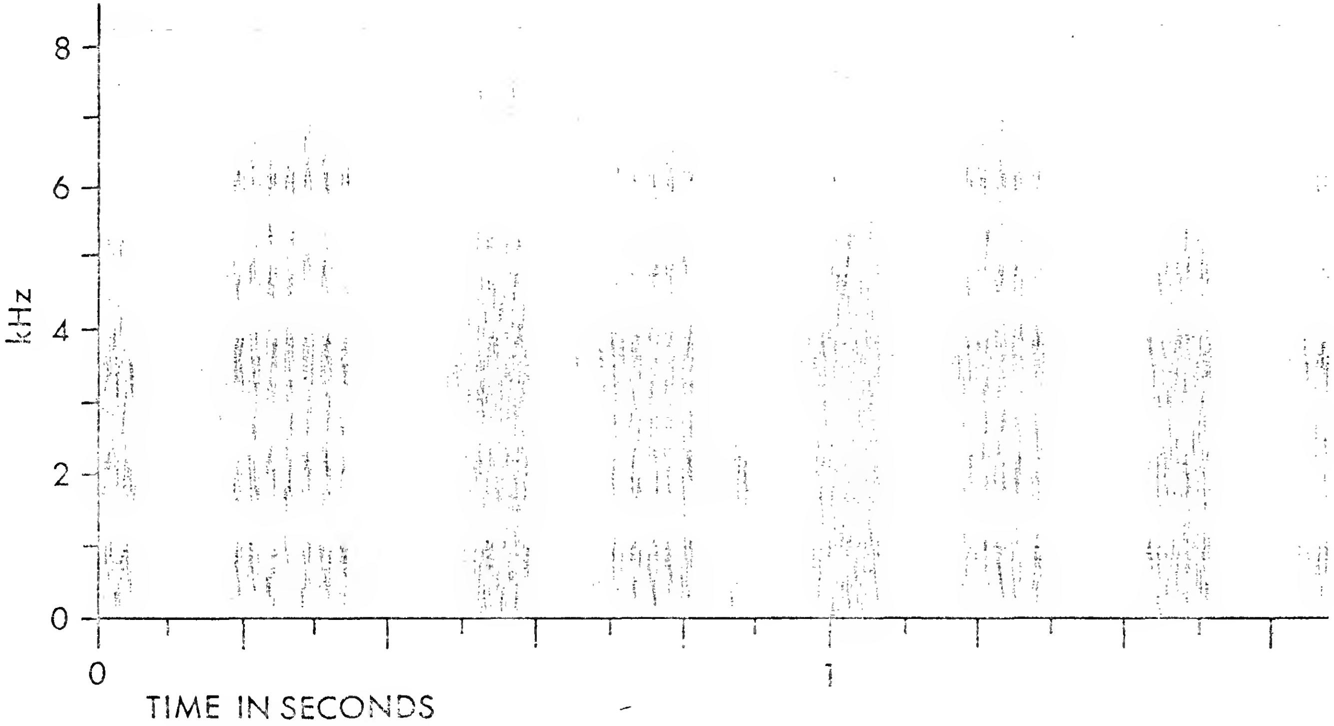

Fig. 17. Passalus punctatostriatus--sounds produced during courtship initiation, Type C by ♂, Type A by ♀, 26°C.

male) turns onto its back and the dorsum-up individual may move the posterior portion of its body onto the ventral surface of the inverted one. Sounds usually cease at this time, and copulation ensues (Fig. 14 c) as described by Schuster (1975).

Post-copulation. Immediately after the aedeagus pulls free of the female, the male usually is very active, walking rapidly, or pivoting on the front legs while rotating the posterior portions of his body left and right. During this time, he often produces a distinctive Type A sound up to 0.5 sec in duration, much longer than the courtship signal, similar to a long disturbance signal (Fig. 6 B). This signal is known for *Passalus punctiger*, *P. affinis*, and *Odontotaenius disjunctus*. Subsequently, other sound types (D, E, C, or B) are produced by the male (Table 4 and Fig. 15 D), many of them of relative low intensity. The male makes sounds both when contacting the female and when alone. He sometimes roots the female, and once a female of *O. disjunctus* produced Type A disturbance-like sounds in this situation. In one case, with *Passalus affinis*, the female aggressed against the male and concurrently produced a series of Type B sounds, typical of female aggression in other contexts. On 1 occasion, copulation was observed in a cage containing 2 males and 1 female (*P. punctiger* from Costa Rica). The post-copulatory male aggressed against the other male with the production of the Type C aggressive signal, despite the fact that he had not aggressed against the latter when contacting him during courtship.

Concerning the function of post-copulatory signals, several suggestions can be made: (1) they keep the pair together, (2) they are non-communicative byproducts, and (3) they repel other individuals. First, Alexander (1967) suggests that, in crickets, post-copulatory signals may keep the female with the male until he is ready to copulate again. This appears not to be the case in passalids for the following reasons: (1) the male locomotes quite actively after copulation, which, in the tunnel system, probably results in his leaving the immediate vicinity of the female, and (2) since the female remains in the tunnel system, she is available for subsequent copulations. Second, the initial Type A sounds produced by the male may be byproducts of the physical movements involved in replacing the aedeagus in its normal position within the body. Third, the aggressive state of a post-copulatory male is suggested by the sound types he produces, his occasional rooting of his mate, and his reaction to another male described in the preceding paragraph. His rapid locomotion after copulation may lead him to traverse much of the tunnel system, and in his aggressive state, to attack any adults that he encounters, probably resulting in departure of those other than his mate from the tunnel system. The post-copulatory signals produced while the male is alone may help maintain him, through auditory feedback, in this excited state during his travels through the tunnels. Those signals produced upon contact with another beetle may aid in repelling it.

Aggression. Aggression in Passalidae is complex, involving 6 types of sounds (C, B*, E, A, D, and F). The particular type produced is apparently dependent on the intensity of the aggression, the role of the producer as aggressor or aggressee, the sex of the aggressor, and the intra- or inter-specific nature of the interaction (Tables 4 and 5). The Type C aggressive signal was first described, for Odontotaenius disjunctus, by Alexander et al. (1963), but in relation to the producers' sex, as it will be here.

Aggression at its highest intensity is characterized by rapid vibration of the antennae of each beetle against the other. The aggressor's mandibles are spread wide and placed under the body of the other beetle. It then jerks upward repeatedly with the head and forebody, rooting the other beetle. Occasionally the mandibles close firmly on an appendage. In these cases, the aggressor may lift the other beetle entirely off the substrate. The beetle attached

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*The Type B aggressive signal is identical to what Schuster and Schuster (1971) referred to as the defensive signal. The pulses they mention have been identified as phonatomes.

may tilt its body down on the side facing the attacker, thus restricting access beneath its body to the attacker's mandibles, or it may run rapidly, thereby breaking contact. The attacker may walk rapidly after a retreating opponent, keeping antennal contact. Sometimes the beetle attacked turns its head to the aggressor and counterattacks. In this case, the animals may meet head to head with much violent vibrating of antennae and interlocking of mandibles (Fig. 18). During intraspecific interactions, the aggressor produces sound Types C, B, or E, while the beetle attacked usually does not stridulate but sometimes produces Type A sounds similar to disturbance signals (Table 4 and Fig 10 A). During interspecific interactions, the aggressor commonly is silent or produces sound often of Type E (Table 5). The aggressee may produce sound Type A.

Usually after contact was broken, following intense aggressive encounters, aggressing individuals of Passalus convexus produced signals (Tables 4 and 5). The sound was always associated with the pushup behavior described previously, but the pushups sometimes occurred without the sound. Pushups were performed in groups of 5 or more.

During mild aggression, 1 beetle, without vibrating its antennae, places its head to the side or rear of another and, with mandibles only slightly spread, lifts its head a few times. The other beetle may move or the aggressor may push on past it. Lifting may occur without sound, or a

Fig. 16. Odontotaenius striatopunctatus during strong mutual aggression. Both are females.

phonatome may accompany each upward movement of the head. In the latter case, the aggressor produces sound Types D (Fig. 19 B), E or, in P. convexus, Type A (Table 4). The aggressee remains silent.

A beetle of a given sex may attack individuals of the same or opposite sex. Male aggressors produce Type C signals, and female aggressors Type B signals, except in a few species (Table 4). In some species, both sexes produce Type E signals. A type C aggressive signal was regularly produced by a female only in Odontotaenius zodiacus. In this species, both male and female make an unusual Type C sound (Fig. 20). In a single case, a female of O. striatopunctatus gave Type C signals when attacking another female. The Type 6 sound was produced by a female in a non-aggressive context only once, a single female of Passalus sp. XV that produced the sound as a disturbance signal (Tables 3 and 4).

The Type B aggressive signal was produced by females except in 1 case, described in Schuster and Schuster (1971), with Passalus punctiger from Costa Rica. The Type B sound is also known from non-aggressive situations, i.e., disturbance, post-copulation, and other solo situations (Tables 3 and 4). In disturbance, it is commonly produced by males as well as females. A post-copulatory male of O. zodiacus produced a Type B signal while separate from the female but a Type C signal when in contact.

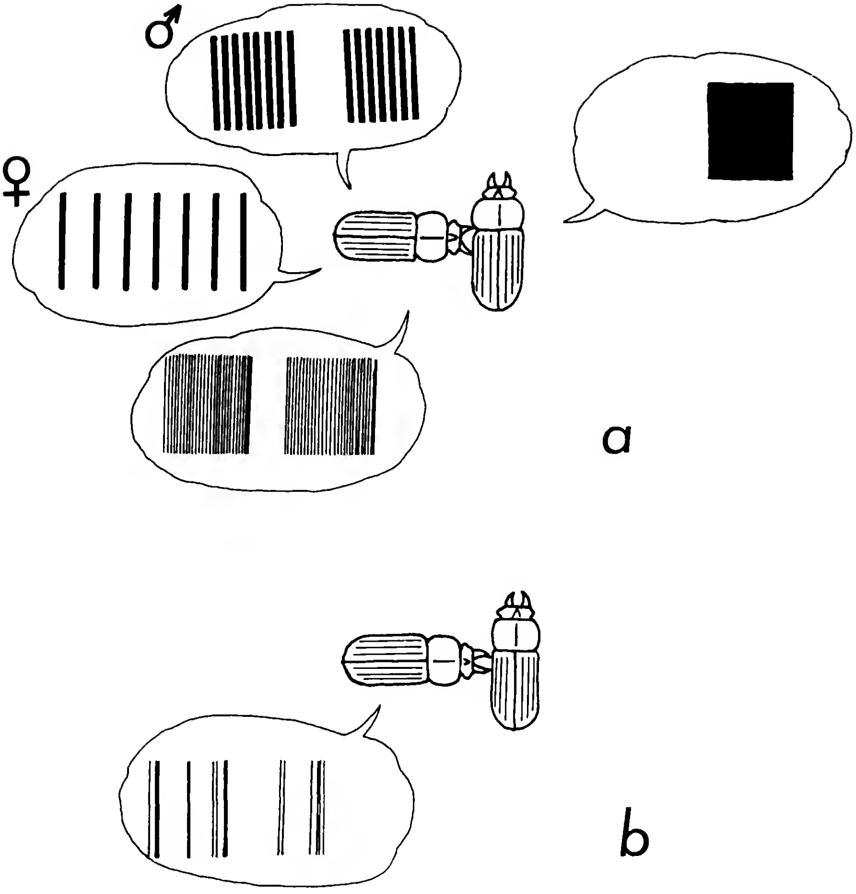

Fig. 19. *Odontotaenius disjunctus*--sound types and position of beetles during aggression by one beetle. (a) Strong aggression, (b) mild aggression.

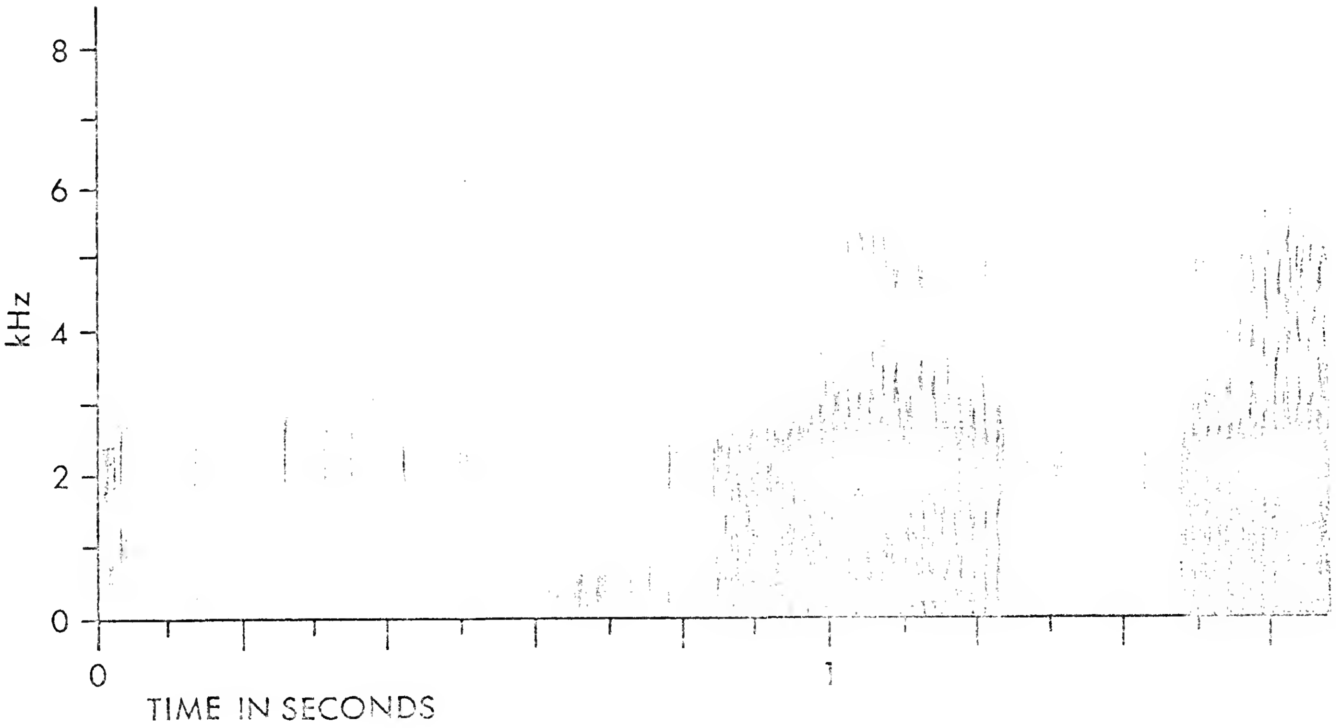

Fig. 20. Odontotaenius zodiacus--audiospectrogram of aggressive signal, 24°C.

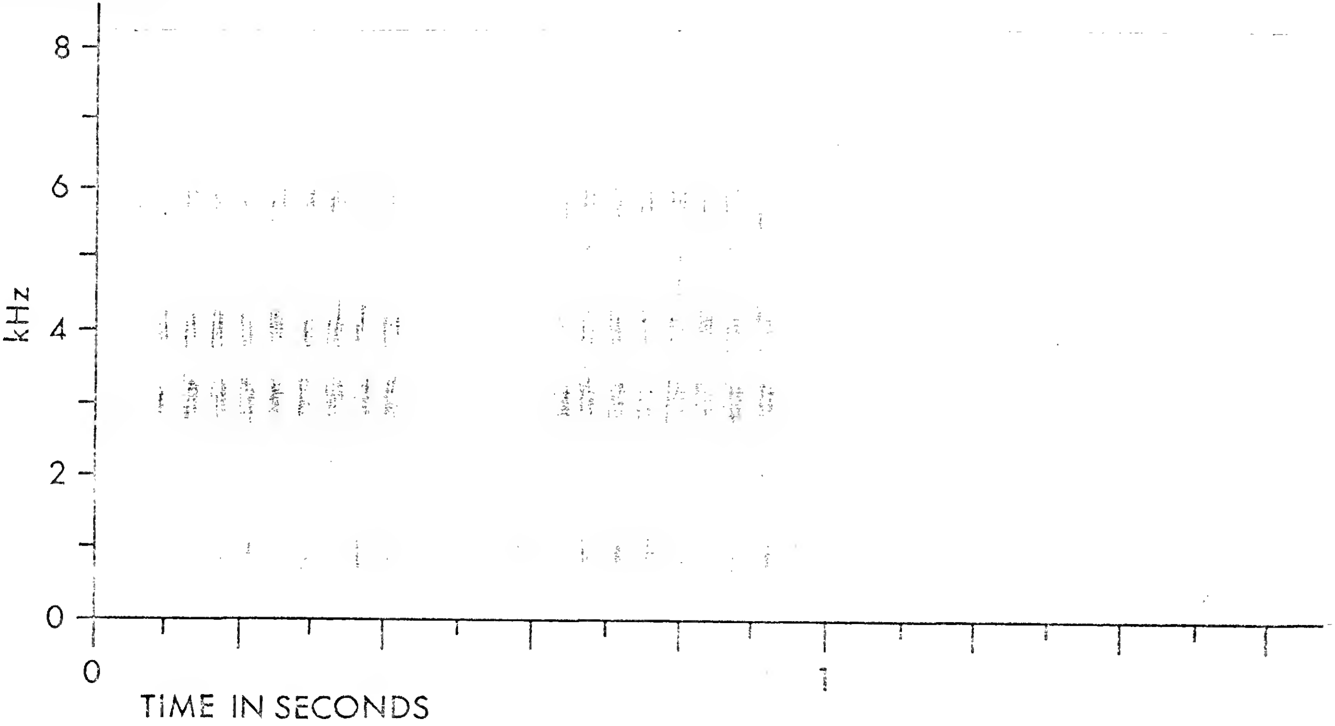

Fig. 21. _Petrejoides_ sp. n.--audiospectrogram of Type C (♂) aggressive signal, 23°C.

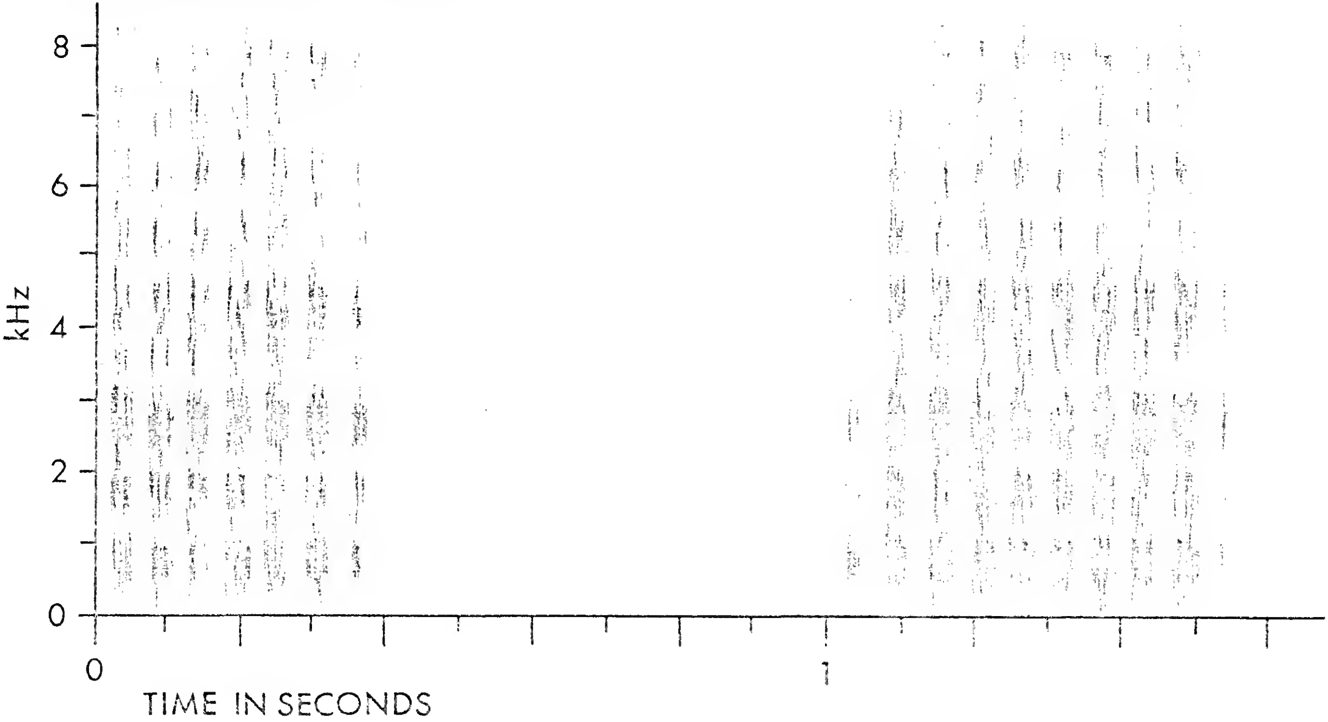

Fig. 22. Passalus affinis--audiospectrogram of aggressive signal, 22°C.

Types B and C aggressive signals, which are characteristically sex-specific, were not produced in interspecific encounters except in 2 cases (Table 5). In 1 case, *O. zodiacus* made its peculiar Type C aggressive signal, but in this species the Type C signal is not sex-specific. In the second case, a female of *Passalus convexus* produced the Type B aggressive signal against *P. coniferus*, but a few minutes earlier she had been producing this signal aggressing against members of her own species.

The role of aggressor can shift in some situations. For exmaple, a female of *P. convexus* was introduced into the petri dish of another isolated female. The occupant attacked the introduced beetle and produced sound Types B and F. After a few minutes, however, the introduced beetle became aggressive and began producing the 2 sound types while the other beetle became passive and silent.

Fourteen species are known to produce Type C sounds during aggression (Table 4). One species, *Odontotaenius zodiacus*, produces a Type C aggressive signal that is very different from those of other species. Its phonatome is 0.31 to 0.41 sec long at 25°C and consists of 15 to 25 very closely spaced bars (Fig. 20). It is similar to the unusual courtship initiation signal of this species (Fig. 8 A), but about half the length. In the Type C aggressive signal common to other species (Figs. 21 and 22), the bar production rate in phonatomes of comparable duration is less than 2/3

Table 5. Sounds produced by aggressor during interspecific mixing experiments in which a single beetle was introduced into a container of 1 or more individuals of a sympatric species.

Species introduced	to Species	Sound types produced by aggressor
Passalus dominicanus	**Passalus affinis*	E
**P. convexus*	*P. interstitialis*	F
P. interstitialis	**P.* near *toriferus*	E
P. interstitialis	**P. punctiger*	-
P. coniferus	**P.* sp. XV	-
P. coniferus	**P. convexus*	BF
P. sp. VIII	**P. coniferus*	-
P. interruptus	**P.* sp. XVII	-
**P. interruptus*	*Veturius platyrhinus*	E
P. interruptus	**V. platyrhinus*	-
P. interruptus	**V. platyrhinus*	-
Veturius platyrhinus	**P. convexus*	A
V. platyrhinus	**P. punctiger*	-
Proculejus brevis	**Odontotaenius zodiacus*	C

*Indicates aggressor.

that of *O. zodiacus*. In these species, the phonatome duration is from 0.09 to 0.39 sec at 25°C and there are from 4 to 14 bars/phonatome. The duration of a phonatome containing a given number of bars at a given temperature varies with the species (Figs. 21 and 22) and the intensity of aggression. The longest signal (0.39 sec with 14 bars) was produced in a violent head-to-head confrontation by 2 males of *O. disjunctus*. Bar duration varies among species from 0.01 to 0.04 sec.

The Type B aggressive signal is known from 8 species (Table 4). The phonatome duration varies with the species from 0.01 to 0.06 sec at 26°C (Fig 7). The rate of phonatome production is greater with more intense aggression. The Type B phonatome of a given species may be quite similar in length to a bar of its Type C aggressive signal, but the rate of Type B phonatome production is never as great as the bar rate of the Type C signal of the same species.

The Type E aggressive signal is known from 8 species (Table 4). Phonatome duration (0.14 to 0.92 sec at 26°C) and number of bars/phonatome vary widely (Fig. 23) even for the same individual. The rate of phonatome production increases with the intensity of aggression.

The Type D aggressive signal is known from 5 species (Table 4). It is a highly variable signal with most bars less than 0.02 sec long (Fig. 9 A). In *Verres hageni*, this signal sometimes tends to be more regular and grade toward a Type B signal.

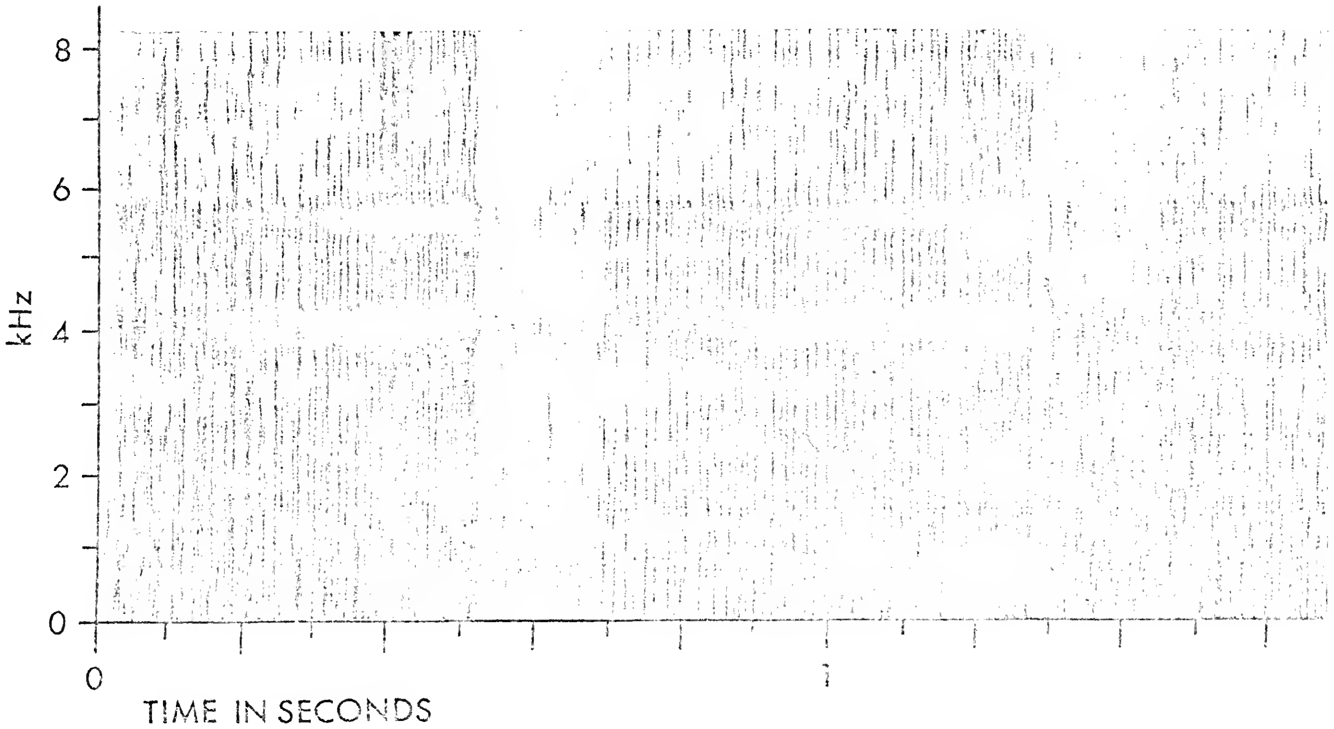

Fig. 23. Passalus affinis--audiospectrograms of Type E aggressive signals of 2 ♀s. (A) 31°C.

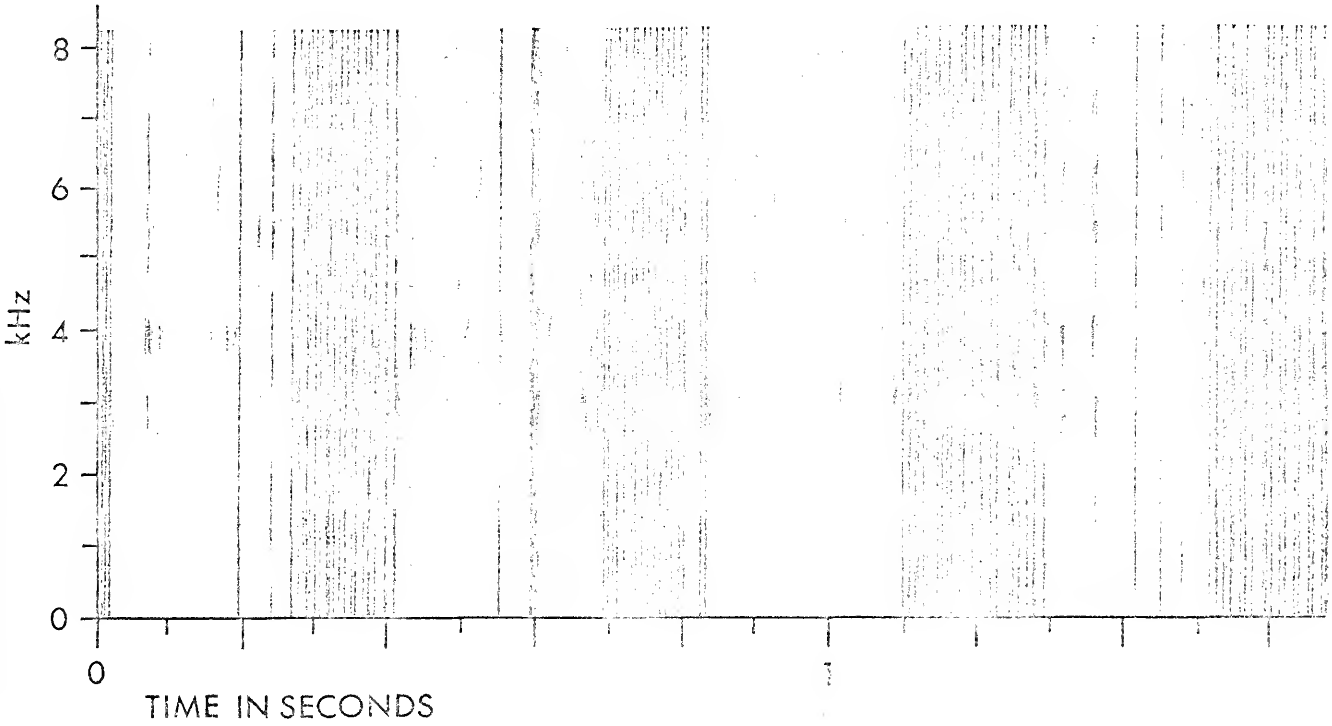

Fig. 23 continued. (B) 29°C

Type A aggressive signals produced by the aggressor are known only from *Passalus convexus*. Type A signals produced by the aggressee are known from 3 species (Table 4). They are all similar to disturbance signals.

Type F aggressive signals are known only from *P. convexus* (Fig. 11), and are always associated with pushups. Pushups occurred after aggression in an unidentified species--*Passalus* (*Pertinax*) sp. XVII--from Peru, but no sound was heard.

Acoustical aggressive signals, in contrast to physical violence, could cause a change in the behavior of the aggressee with less risk of injury to either it or the aggressor. The beetle attacked may be informed by the aggressor's acoustical signals of the latter's sex and mating potential, with the result being (1) the beetle attacked leaving the tunnel system, (2) temporary separation, or (3) a shift to mating behavior.

The aggressor usually has its head to the side or rear of the other animal. In this position, through repeated antennal contact, it receives chemical and tactile information concerning the sex and other attributes of the beetle contacted. The aggressee, however, has little antennal contact with the aggressor and apparently lacks chemical and tactile information concerning the latter. A beetle's lack of information concerning an individual at its side or rear is indicated by the following: if 1 beetle is aggressing against a second and contact is temporarily broken, the second may repeatedly antennate the first from side or rear without being attacked, but the moment the first antennates the second, the attack is resumed. Lacking rapid chemical or tactile means of communication, the aggressor may pass information to the aggressee by sound.

Information that might be conveyed by the intensely aggressive signals (Types C, B, and E) is given in Table 6 along with the possible response of the aggressee to this information. Responses are of 2 kinds: (1) the aggressee may leave the tunnel system, or (2) the aggressee may remain in the same tunnel system and eventually mate with the aggressor. A variety of combinations of signal and aggressee's sex give information leading to the first response but only 2 combinations (signal C and female aggressee, or signal B and male aggressee) give information leading to the second.

Several reasons may be given to explain why more than 1 signal (Types C, B, or E) may cause the aggressee to leave the tunnel system. First, in a male-female encounter, signals B or C, without E, probably would not have this effect because they would indicate that the aggressor was a potential mate. The signal E, however, could cause the aggressee to leave by indicating that the aggressor was unlikely to be a potential mate and that a member of the aggressee's sex already occupied the tunnel system. Second, in a male-male or female-female encounter, Type E could have the same meaning. It might, however, be less effective than Types C or B because the latter could indicate that the aggressor was of the same sex as the aggressee and therefore under no circumstances a potential mate.

If a male producing the Type C signal aggresses strongly against a female, she sometimes turns her head to him and produces a Type B signal. When this happens, the male usually stops aggressing, and the individuals separate or the male initiates courtship. This suggests that the Type C aggressive signal might stimulate a female to identify herself as such (or reaffirm her sexual identity) by producing the Type B signal. The Type B signal apparently then causes the male to cease aggression (which might drive the female from the tunnel system), and the 2 remain in the same tunnel system until they are ready to mate. An example of this is the following: A female of Odontotaenius disjunctus which had been found as the only individual in a new colony, and a male found similarly, were caged separately for a month. Then, the female was placed into the male's container. Upon contact, the beetles vibrated their antennae vigorously against each other as in aggression, but without lifting or rooting. First, the female contacted the male, her head to his side, without stridulation. Sixteen and one-half seconds later, the male placed his head to the female's side and produced 4 Type C phonatomes. At this point, the female turned so that the beetles were head to head and, at 18 sec after first contact, produced 2 short sequences of Type B phonatomes, the first of which overlapped the last 2 phonatomes of the male. Total period of male and female stridulation was 6 sec. This was followed by silence while the beetles antennated each other. The silence was broken by one Type C phonatome and, 83 sec after first contact, 3 courtship phonatomes. Continuous production of male and female courtship signals began about 125 sec after first contact. When the beetles separated during courtship, the male would produce 1 or 2 Type C phonatomes upon re-contact, before resuming the Type A sequence. The male turned onto its back 24 times (the female once) before copulation occurred 1 hr and 20 min following first contact. The sounds produced during mild aggression (Types D and E) may function as low-energy reaffirmation of a previously established dominance hierarchy. This may be important in a tunnel system occupied by a pair with many adult progeny.

Disturbance. Passalids, like many other insects, produce sounds when handled, poked, or blown upon, and these have been called disturbance or alarm signals (Alexander, 1967). I recorded disturbance signals from 42 species of New World Passalidae (Table 3). The commonest signal was a Type A sound; it was the only disturbance signal given by 29 species; it occurred in combination with 1 or more other sound types in 10 species; and phonatomes intermediate between Type A and Type C comprised the disturbance signals of 2 species. One species, Proculejus brevis, had only Type B disturbance signals.

Type A sounds similar to those made when a passalid is handled are produced in the following situations: (1) by beetles when 1 slips and falls on another, (2) by a passalid being attacked by a predator, (3) by a beetle contacting or being attacked by other species of Passalidae, and (4) by an individual being attacked by conspecifics. Type A sounds were produced in laboratory containers in all these situations, and were observed in the field for the last one mentioned. All are associated with violence or aggression. Though Type A is the commonest sound, Types B, C, and F have also been produced during and following disturbance by an observer. These sounds, too, are found most commonly associated with aggression.

The phonatome duration for Type A disturbance signals ranges from 0.06 to 0.58 sec at 26°C. Wide variation in duration at a given temperature occurs, even for an individual beetle (e.g., 0.07 to 0.31 sec at 29°C for an individual of Passalus affinis). Nevertheless, some species are apparently characterized by relatively long disturbance signals (mode greater than 0.2 sec at 26°C), others by intermediate (mode 0.1 to 0.2 sec) or short signals (mode less than 0.1 sec).

Type B sounds, similar, if not identical, to those of female aggressive signals, as well as Type A sounds, are produced, following disturbance, by *Passalus* sp. XV, *P. spinifer*, *P. interstitialis*, *P. punctatostriatus*, and *Odontotaenius striatopunctatus*. With these *Passalus* species, a disturbance sequence starts with Type A phonatomes, and is followed by an abrupt switch to Type B phonatomes (Figs. 24 and 25). I observed this behavior in individuals of *P. interstitialis* from Peru, Panama, and Jamaica, indicating that it is common behavior in the species despite its broad range and disjunct populations. *O. striatopunctatus* often alternates Type A and Type B sequences.

A Type C sound, apparently identical with that of the male aggressive signal, was occasionally produced in addition to the more common Type A signal by approximately 25% of the individuals of *Petrejoides* sp. n., *Heliscus* sp. n., *Odontoaenius zodiacus*, *Spasalus crenatus*, *Passalus* sp. XV, and *Passalus caelatus*. In the case of 1 individual of *P. caelatus* from Peru, I observed Type F sounds, accompanied by pushups, after disturbance. The pair of "clicks" was produced between 2 Type A phonatomes at several points in a sequence of predominantly Type A sounds. Five other individuals of this species failed to produce Type F disturbance signals, perhaps suggesting that Type F sounds are more characteristic of another context, perhaps of aggressive situations, as in *P. convexus*.

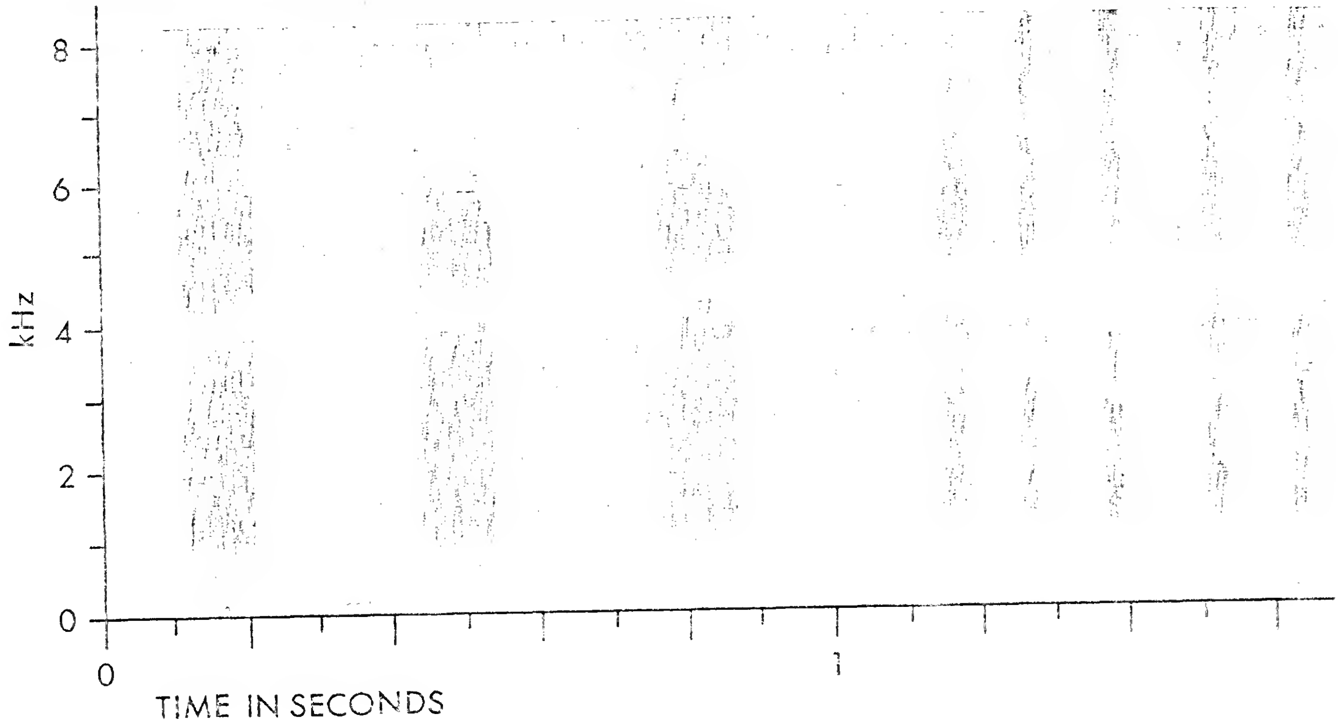

Fig. 24. *Passalus punctatostriatus*--audiospectrogram of sequence of Type A to Type B disturbance signals of one beetle, 22.5°C.

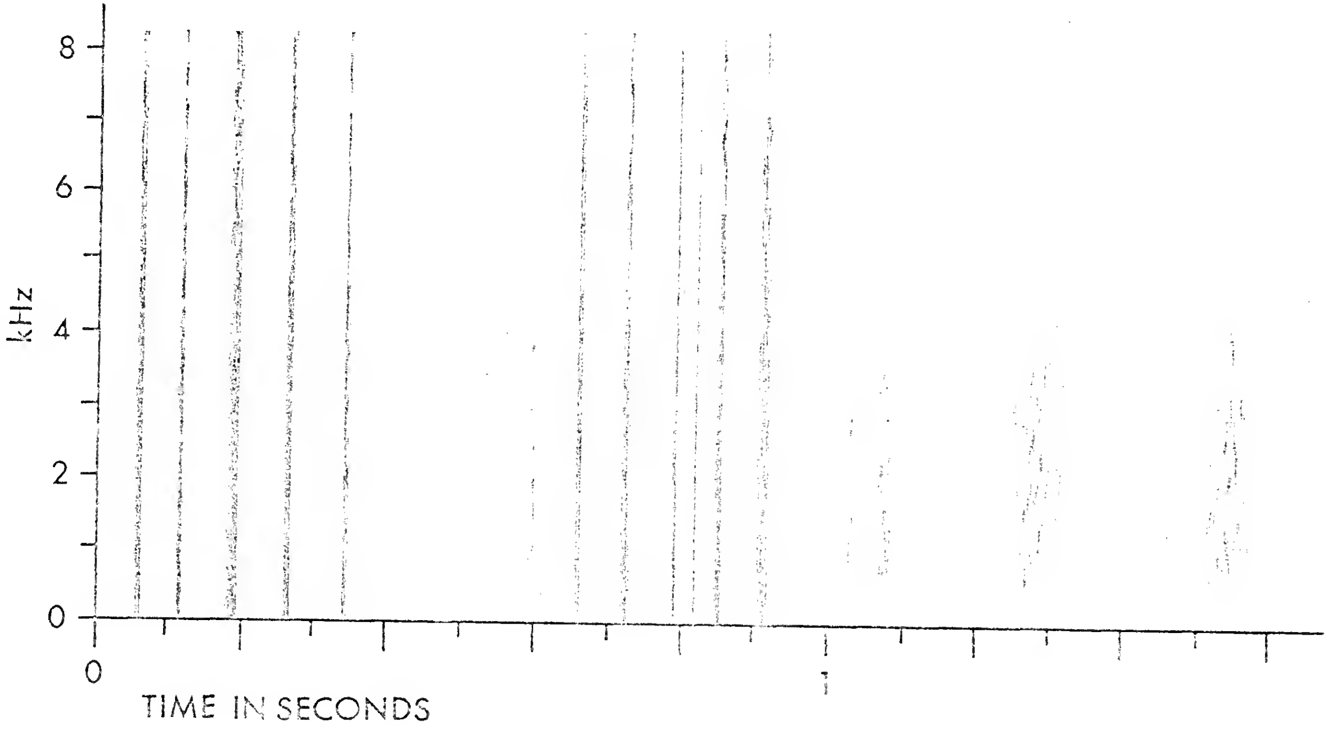

Fig. 25. *Passalus interstitialis*--audiospectrogram of sequence of Type B to Type A disturbance signals of one beetle, 29.5°C.

Concerning the 2 species that produce signals intermediate between Type A and Type C, the phonatomes of *Passalus inops* begin as a normal Type A sound, but end with 3 or 4 short bars (Fig. 26). *Oileus nonstriatus* produces a sound that is composed of short bars which run together in part of the phonatome (Fig. 27).

Individuals of some species do not make disturbance signals when initially disturbed. The beetle retracts its legs under and flat against its body and holds itself immobile (Fig. 28). If I extend its leg, it will draw the limb back under its body again. No sound is made while in this position. I have, at times, removed 1 of these beetles from its petri dish thinking it dead, only to find it walking around a few minutes later. This behavior pattern has been observed only in *Ptichopus angulatus*, and in members of the subgenus *Pertinax* of the genus *Passalus*: *P. convexus*, *P. punctatostriatus*, and an unidentified species from Peru (*Passalus* sp. XVII).

Baker (1971) has made the only modern analysis of disturbance signals in Old World Passalidae. He treats 3 species: *Pentalobus palini* Perch., *P. barbatus* F., and *P. savagei* Perch. Their signals appear to consist of Type A sounds, as with New World passalids. One species, *P. savagei*, also makes a Type B disturbance signal, as do a few New World species.

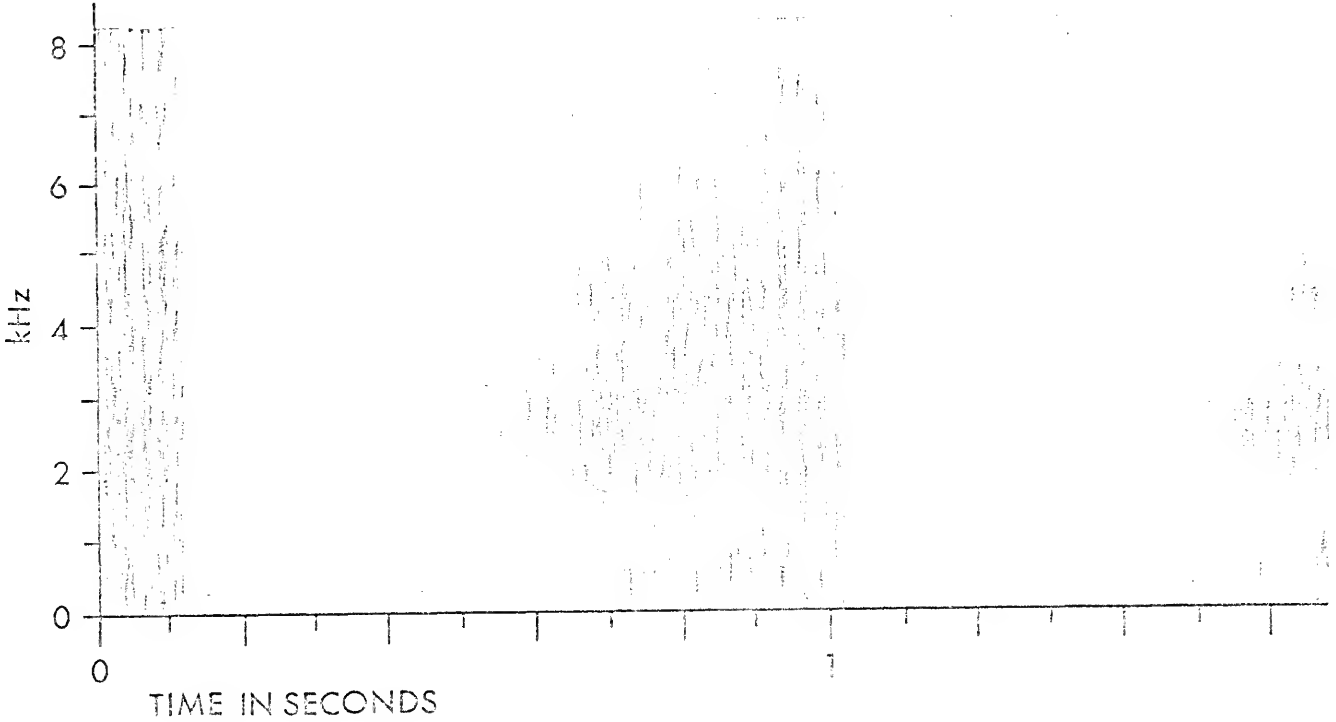

Fig. 26. _Passalus inops_--audiospectrogram of disturbance signal, 23.5°C.

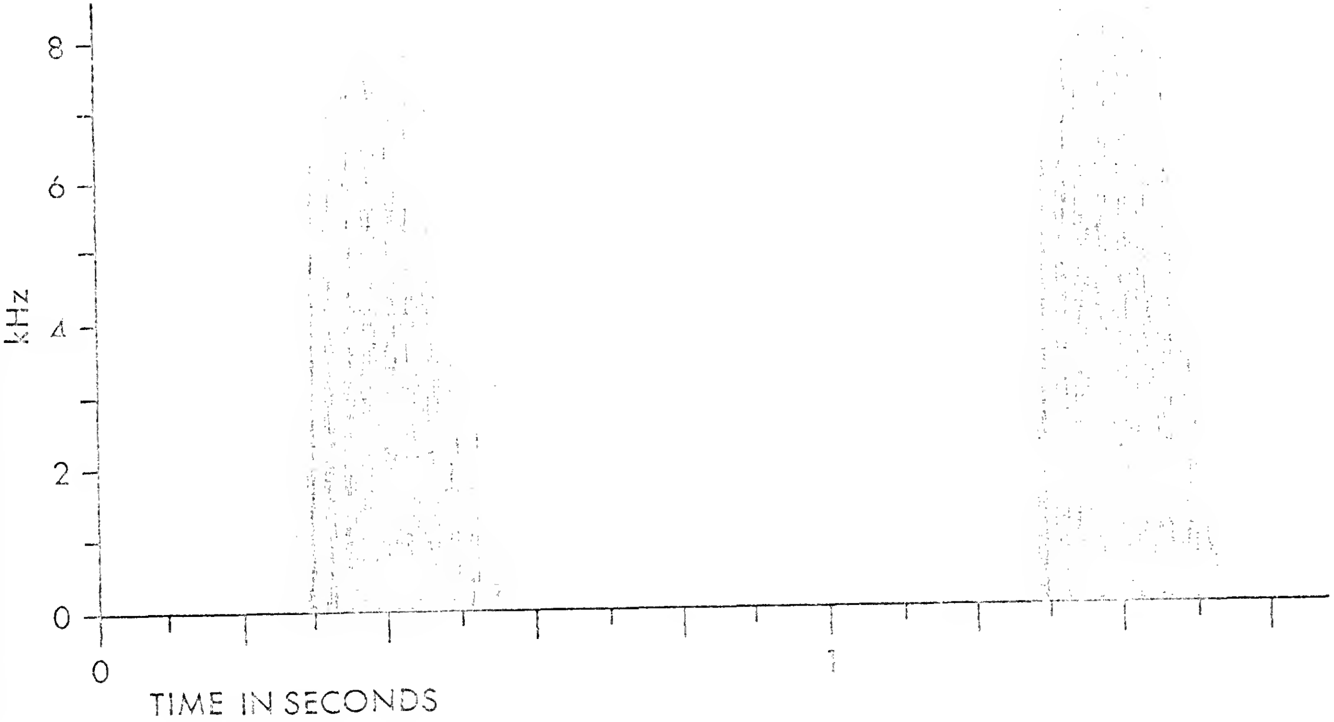

Fig. 27. _Oileus nonstriatus_--audiospectrogram of disturbance signal, 25.5°C.

Fig. 28. *Passalus punctatostriatus*--immobile position assumed when disturbed by observer.

I observed 2 cases in which disturbance-like signals were produced when beetles were attacked by a reduviid, *Melanolestes picipes* (Herrich-Schaeffer), which is found in *Odontotaenius disjunctus* tunnels. The attacks took place in a petri dish. The phonatomes were particularly long Type A sounds (0.43 to 0.46 sec compared with a range for disturbance phonatomes of approximately 0.11 to 0.32 sec at 22 1/2°C), and did not appear to deter the attack in any way. The sound continued for minutes after the reduviid had inserted its beak. In 1 case, a second beetle antennated the beetle under attack but otherwide there was no apparent change in its behavior.

Three suggestions may be made concerning the function of sounds produced in response to disturbance by a member of another species: (1) the sound will cause the predator or other organism that contacts the beetle to drop it or leave it alone, (2) it acts as a warning to conspecifics, and (3) it is a misplaced response from intraspecific interactions.

The third idea is suggested by the fact that, in intraspecific interactions, Type A disturbance-like signals are produced by the aggressee while retreating, Type B sounds are given by a female in response to male aggression, and Type C sounds are produced by a male aggressor. I suppose the violent stimulus of disturbance by an individual of another species may trigger the same response as does the violent stimulus of aggression by a conspecific.

The second idea, a warning signal, is not supported by any clear evidence, except in termites (Alexander, 1967). Nor is it supported by my observations of Passalidae. When a disturbed passalid is held near other passalids, larvae or adults, one notices no change in their behavior, even when the disturbed beetle is pressed against the substrate to allow for substrate transmission of the disturbance signals. This was true with laboratory colonies in which adults were successfully raising young, the disturbed beetle being a member of the same colony or of another colony. In the field, I pressed a beetle against a log and monitored the log for acoustical signals or sounds of activity (feet-scraping, etc.). I detected no sounds other than that of the disturbed beetle, yet the log was subsequently found to be occupied by passalids, which made clearly audible signals upon the introduction of another individual into their tunnel system.

The first idea, that of predator repellance, has never been proved for any arthropod (Alexander, 1967) and certainly didn't function as such in the attack on passalids by the reduviid mentioned previously. With some predators, however, the result might have been different as suggested by the following argument: Many other species of insects produce disturbance sounds that are quite similar to those produced by Passalidae. All have about the same duration, and broad frequency spectrum, e.g., Hydrophilidae (Ryker, 1972), Cerambycidae (Alexander et al., 1963), Mutillidae (Fig. 29). This suggests the possibility of sound mimicry. Some insects producing these sounds can inflict a nasty sting or bite (e.g., Mutillidae). Mutillids don't live in passalid tunnels, but the reduviid mentioned previously, Melanolestes picipes, does and will inflict a painful bite on a human (and presumably any mammalian predator). It also produces disturbance sounds similar to passalids' (Fig. 30). Lane and Rothschild (1965) mentioned a similar case of audiomimicry concerning a silphid bettle mimicking a bumblebee. This still doesn't explain why hydrophilid, etc., sounds are similar to passalids', unless they are similar due to functional convergence (by both models and mimics) in a predator-repelling situation.

Other solo. Beetles not in contact with other individuals produce sounds rarely, except after copulation. Alone after copulation, males produced sound Types A, D, E, and B. A few minutes after an aggressive encounter, an individual of O. disjunctus produced the Type D sound while feeding alone. These cases are included in Table 4 under post-copulation and mild aggression, respectively; only signals not directly associated with mating, aggression, or disturbance are listed in the column "Other solo."

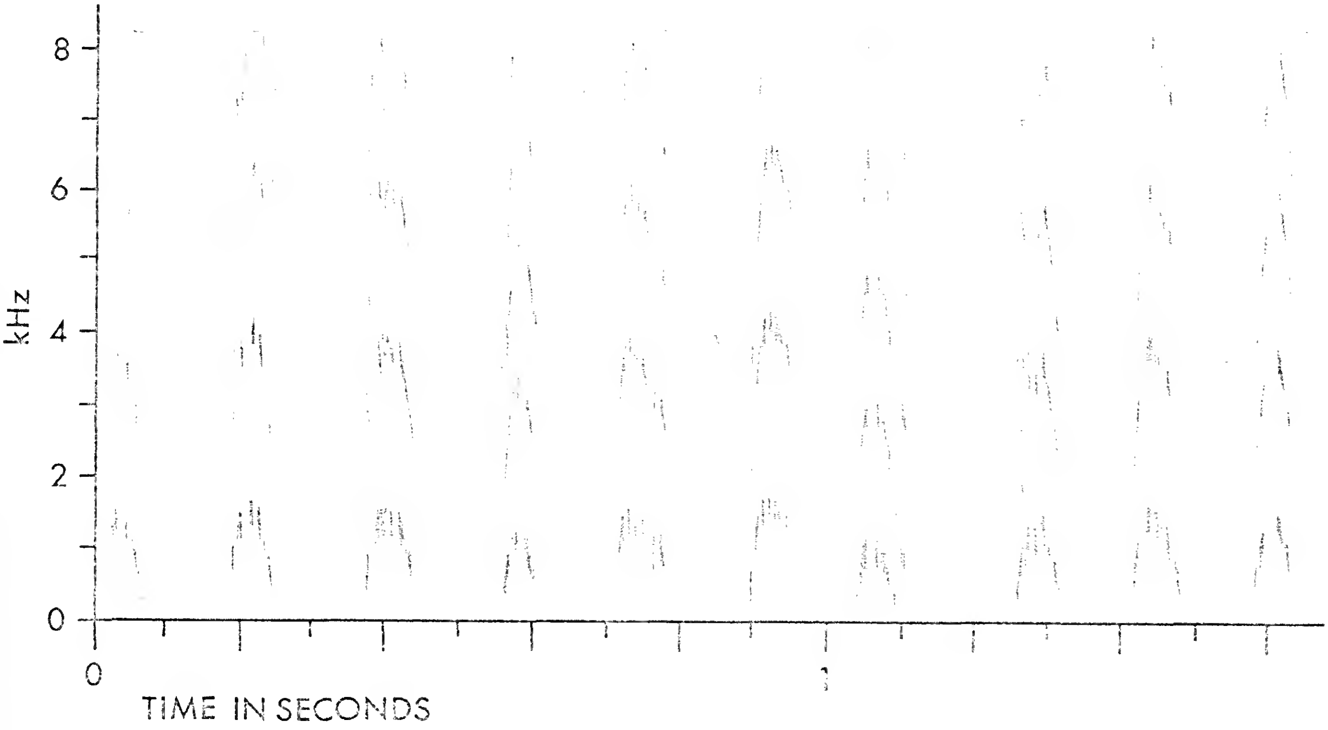

Fig. 29. Audiospectrogram of disturbance signal of ♂ mutillid wasp. Females also produce sound.

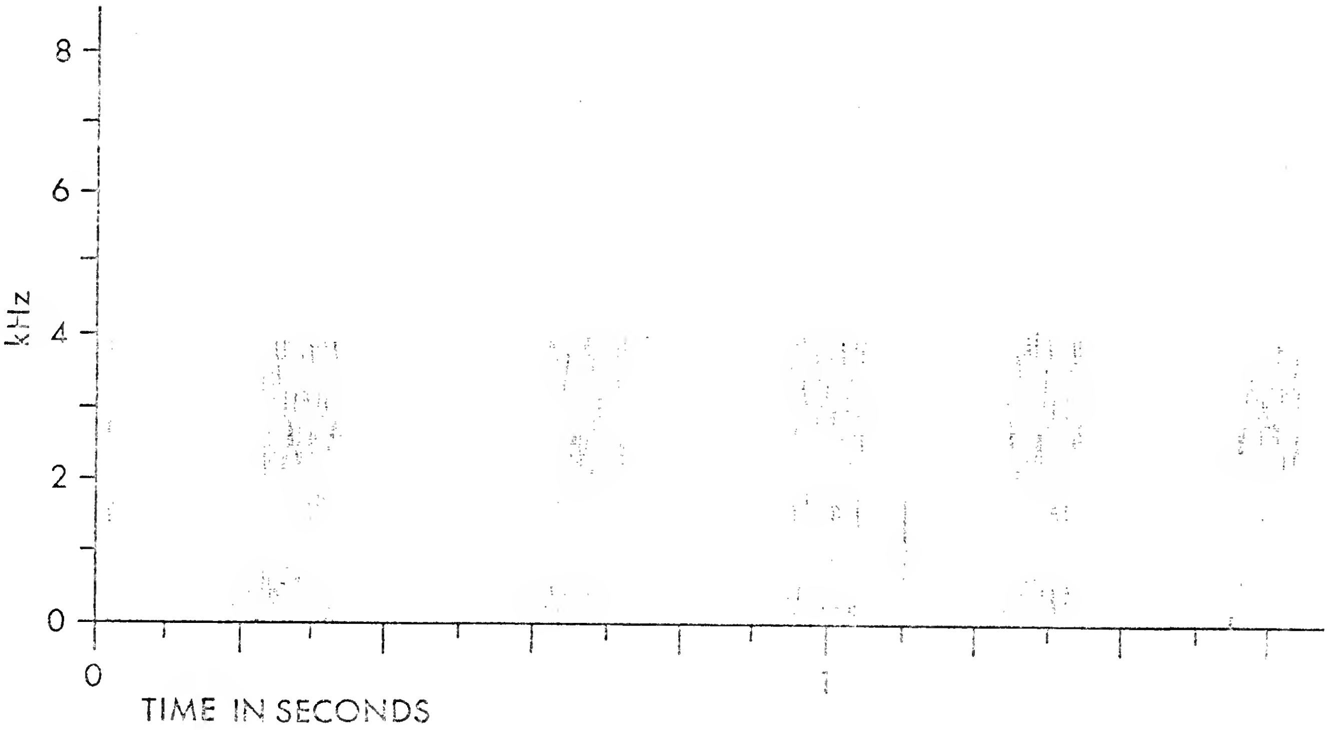

Fig. 30. *Melanolestes picipes* (Reduviidae)--audiospectrogram of disturbance signal 22.5°C.

Type B sounds were produced by an isolated beetle of *Passalus inops*, of *P. dominicanus*, and of *O. disjunctus* while walking in their containers. In the case of *P. inops*, a female had been placed in a large petri dish 5 to 10 min before it began making the sound. As it made the sound, it walked around the circumference of the dish, mandibles closed and antennae not vibrating. When I tapped on the table, it would stop producing the sound. Sound Type G was produced by individuals feeding alone, and Types D and E by beetles feeding or inactive. The distinctive Type G sounds (Fig. 12) were regularly produced (1 or 2 per min) by 2 separate individuals of *Passalus punctiger* from northern Mexico after new wood was added to their containers.

Sounds produced by solitary individuals might serve as a means of spacing beetles in logs, perhaps similar to the situation for *Dendroctonus* (Scolytidae), as described by Rudinsky and Michael (1973).

Larval interactions. Larvae produce sounds in at least 3 situations: (1) Most larvae will produce sounds when disturbed by the observer handling or blowing upon them. (2) Larvae of *Passalus affinis* occasionally made sounds while mouthing wood or frass and not in contact with other individuals. (3) *Odontotaenius disjunctus* larvae often stridulate when in contact with adults (Fig. 14) and occasionally with other larvae. *P. affinis* larvae also frequently stridulated when contacting adults. The sounds are made when the head of the larva is touching the other individual.

On some occasions, a larva repeatedly jerked its head sideways or downward against another individual. O. disjunctus larvae did this against other larvae and adults. Third instar P. affinis larva stridulated while knocking their heads against adults as well as without this knocking.

A "congregating" function has often been attributed to the larval sounds (Alexander et al., 1963, and others); Ohaus (1900) describes a situation in which adults and other larvae supposedly called separated larvae to the group and to "safety" under a piece of wood. Since larval sounds are much less intense than adult sounds, I doubt that they can be received over much distance; they are probably detected primarily when in physical contact with other individuals. In this situation, they may reaffirm to the receiver the larva's presence and identify it as a passalid larva. If larvae or adults would locomote extensively until they received such signals, the signals would aid in keeping a group together. Also, sound may serve as a stimulus to the adults to increase production of frass and fecal material, which are the primary larval food.

Field experiments. Attempts were made to study passalid sounds in the field, in order to facilitate interpretation of laboratory observations. This was done in 2 ways:

(1) by monitoring logs for spontaneous sounds, and (2) by introducing beetles into field logs (since most of the sounds heard in the laboratory were a result of mixing beetles not previously in contact). The studies were carried out on logs occupied by *Odontotaenius disjunctus* in Florida, and by *Passalus affinis* in the Dominican Republic.

During a period of 15 to 75 min immediately before introducing beetles into occupied logs in the field, these logs were monitored for spontaneous sounds. The only sounds heard were Type D during a period of about 5 min on 22 July 1973 in a log occupied by *O. disjunctus*. The paucity of spontaneous sounds was not surprising, since laboratory observations of *O. disjunctus* revealed an average of only 15 sec spontaneous stridulation/pair/hr, mostly produced in long courtship sequences by a few beetles. This average was determined in a study of 10 pairs over a total of 70 hr, including all times of day.

The sounds produced after single beetles were introduced into the logs are shown in Table 7. Most of these sounds were associated with aggression. Both male and female occupants aggressed against the intruder, regardless of the latter's sex. Type E aggressive signals were apparently made in all cases. When it was possible to see which beetles produced the sounds, it was noted that both male and female occupants made Type E signals. Types B and

Table 6. Information possibly conveyed by acoustical signals during intense aggression and possible response of aggressee to signals.

Aggressor's signal	to Aggressee	Possible information conveyed	Result
C	♀	Aggressor is a ♂ (∴ a potential mate)	♀ produces Type B signal. This is followed by: (1) temporary separation, or (2) initiation of courtship.
C or C + E	♂	Aggressor is a ♂ (∴ not a potential mate and tunnel system occupied by ♂)	Aggressee leaves tunnel system.
C + E	♀	Aggressor is a ♂, but not a potential mate because member of aggressee's sex present in tunnel system	Aggressee leaves tunnel system.
E	♂ OR ♀	Aggressor is not a potential mate, because member of aggressee's sex present in tunnel system	Aggressee leaves tunnel system
B	♂	Aggressor is a ♀ (∴ a potential mate)	Cessation of ♂'s simultaneous aggression followed by (1) temporary separation or (2) initiation of courtship.

Table 6 (continued)

Aggressor's signal	to	Aggressee	Possible information conveyed	Result
B or B + E		♀	Aggressor is a ♀ (∴ not a potential mate and tunnel system occupied by ♀)	Aggressee leaves tunnel system.
B + E		♂	Aggressor is a ♀ , but not a potential mate, because member of aggressee's sex present in tunnel system	Aggressee leaves tunnel system.

Table 7. Sounds produced by passalids during field log introduction experiments in Florida and the Dominican Republic.

Beetle introduced to	Log occupants	Sounds produced	Date
Odontotaenius disjunctus (Florida)			
♂	♂ + ♀	C B E? A	4 Nov. 1972
♂	♂ + ♀ + eggs	E	1 Apr. 1973
♂	♂ + ♀ + eggs, larvae	E A	6 May 1973
♂	♂ + ♀	E	6 Oct. 1973
♀	♂ + ♀	B E A	6 Oct. 1973
♀	♂ + ♀	C B E A	22 July 1973
♀	♀	-	4 Nov. 1973
♂,♀	-	-	1973*
Passalus affinis (Dominican Republic)			
♂	♂ + ♀ + larvae	E A	16 Sept.1973
♀	♂ + ♀ + larvae	E	16 Sept.1973

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*Six or more introductions were made into tunnel systems that proved to be unoccupied.

C aggressive signals were made against intruders of either sex in O. disjunctus. Type A, disturbance-like signals, were made by the intruder in 4 cases. The intruder either left the log (7 cases) or left the vicinity of the occupants (e.g., in 1 case the intruder and occupants were found at opposite ends of the tunnel system, 2 feet apart). In 1 case, a few Type A courtship-like phonatomes were heard before aggression began, though it was impossible to tell whether these were made in an interaction involving only the original occupants or 1 involving the intruder.

In 1 experiment, it was impossible to force a female into a tunnel. She would wedge herself in the entrance and, upon release, she would back out. Subsequent examination of the log revealed it was occupied by a single female in a tunnel system only 10 cm long. No sounds were heard, suggesting that the introduced beetle may have contacted the rear of the occupant and, through chemical or tactile signals, determined the system was already occupied by a female.

These experiements indicate a definite territoriality in Passalidae. The reproductive (evolutionary) advantage of an occupant of a tunnel system attacking an intruder of the same sex is obvious. But why should either member of a pair attack an intruder of the opposite sex? To aid in answering this question, I set up 2 trays (44 cm x 34 cm x 2 cm) filled with pieces of rotting wood, each covered with a glass plate. The glass was covered with opaque paper which could be removed for observation. In one tray, I placed a male and 3 females. In the other, I placed a male and a female. At least 13 eggs were laid in the tray with the pair of beetles, and 7 eggs in the other tray. Five larvae belonging to the single pair reached adulthood. None of the larvae in the other tray even reached pupation, possibly due to cannibalism by the adults, such as Gray (1946) noted when adults and larvae of *Odontotaenius disjunctus* were caged together. If such high mortality associated with non-related beetles in the same tunnel system occurred in nature, it would be advantageous for *either* parent to attack non-related individuals of either sex present in their tunnel system.

DISCUSSION AND CONCLUSIONS

Compared to insects of other families, passalids are remarkably homogeneous in behavior, habitat selection, and life cycle as well as morphology. The great majority are tropical and live in warm, moist habitats associated with decomposing plant matter, usually rotting wood. Few species are found in temperate regions, above 2800 m altitude, or in deserts. Seasonal cold or dryness may cause life cycle periodicity. Black adults leave the vicinity of old colonies by walking or, in some species, flying. Either sex may initiate a colony and is subsequently joined by an individual of the opposite sex. Eggs are placed in a nest within the tunnel system. The parents cooperate in rearing the young by providing food for the larvae and helping them to form pupal cases. After emergence, the adult offspring may remain in the tunnel system with the parents. This overlap of generations and cooperative behavior characterize the Passalidae at a stage between primitive subsocial and truly social behavior. Adult passalids can live for more than 2 years and produce more than 1 brood. Much of their behavior includes acoustical signals produced by larvae and adults of both sexes.

By glancing at Tables 3 and 4, one can see that the same sound type is found in a given context in most species, i.e., there is a great deal of similarity in the signals of different species. This is in contrast to the variety found in some groups, for example, Orthoptera and Cicadidae. In these, acoustical calling signals are the primary means of long distance attraction between the sexes; the development of species-specific differences in such signals is selectively advantageous because they will bring together only conspecifics. In Passalidae, there are no acoustical calling signals. Perhaps pheromones are used in this context. Yet, there are courtship signals, and Alexander et al. (1963) postulated that, in closely related species of sound-producing beetles occupying together restricted niches (e.g., dung, rotting logs), courtship signals should evolve towards species-specificity due to the high probability of chance encounter between male and female of different species. In Passalidae, up to 10 species may occupy the same rotting log (Luederwaldt, 1931), yet courtship signals are similar. However, I have never found the tunnel systems of 2 species definitely interconnecting, even though approaching within 1 1/2 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 (Rudinsky and Michael, 1973). The silent aggression in the interspecific mixing experiments indicates that species recognition, when passalids contact, occurs without the aid of sounds.

The interspecific similarity in structure of passalid sounds evident between the 2 New World tribes indicates that these patterns are quite ancient and have a common origin. Investigation to determine if Old World Passalidae, especially those of the other subfamily Aulacocyclinae, differ from this general pattern, may help clarify relationships among Passalidae at higher taxonomic levels and possibly provide suggestions on the evolutionary origin of passalids and their sounds.

Two members of the genus *Odontotaenius* displayed the most strikingly different patterns of sound production of all species studied. One, *O. zodiacus*, is a species confined to the temperate cloud forests of pine and beech of the Sierra Madre Oriental of Mexico. Its Type C sound (Fig. 8 A) was unique, and females of *O. zodiacus* were the only ones which regularly produced Type C aggressive signals. Males of *O. zodiacus* produced no acoustical courtship signals. In the second species, *O. striatopunctatus*, both male and female courtship signals were lacking, as well as the courtship initiaiton signal. Since the individuals studied of this species belonged to a disjunct population in northern Mexico, one wonders if the lack of sounds in the mating sequence is normal for the species over its entire range, which extends to Costa Rica.

In some species of Passalidae, the wings are reduced to thin straps, useless for flight, with only the stridulatory structures remaining at the enlarged distal portion (Arrow, 1904). I only have data on acoustical signals for 2 species with this wing reduction, *Proculejus brevis*, and *Oileus nonstriatus*. Both species produce disturbance sounds differing from those of other species. *P. brevis*, in particular, was the single species that produced only Type B disturbance signals; it produced no Type A disturbance signals. A Type A phonatome is longer than a Type B, and wing reduction, with possible reduction of the stridularoty surface, might have made it impossible for this species to produce a Type A sound. If it cannot, therefore, produce Type A courtship signals, the question arises, does it produce a Type B sound instead of a Type A in courtship as it does in disturbance? Though the difference between Type A and Type B sounds is based on length, the separation of Type A from Type B at 0.06 sec was not an arbitrary decision. All single bar phonatomes fall into 2 distinct groups (for example, in a single sequence--Fig. 25), the 0.06 sec duration lying between these groups in all species studied. The long group is characterized by the courtship signal (as well as most disturbance signals); the short group is characterized by the female aggressive signal, the bar length of which is similar to that of the bars of the male aggressive signal. Therefore, any individual that produces a courtship signal less than 0.06 sec duration runs the risk of it being misinterpreted as aggression.

Alexander (1967) stated that there are no acoustical courtship signals known for any female arthropod. Females producing courtship signals are now known from Cerambycidae (Michelsen, 1966), Scolytidae (Wilkinson, McClelland, Murillo, and Ostmark, 1967) as well as Passalidae. In addition, female passalids, unlike Orthoptera, have a repertoire in aggressive and disturbance situations of similar extent to that of the male. This includes a female aggressive signal (Type C), as well as various signals produced in common (e.g., the Type E aggressive signal and the Type A disturbance signal).

The extent of the repertoire of a single species (Tables 3 and 4) may be illustrated with *Odontotaenius disjunctus*, the species that I observed most intensively. In 11 behavioral contexts, it produced 5 of the sound types for a total of 14 different signals.

1. Courtship Initiation--Type C phonatomes similar to those of male aggression.
2. Courtship (male)--Type A phonatomes 0.07 to 0.08 sec duration at 26°C.
3. Courtship (female)--Type A phonatomes about 0.08 sec duration at 26°C.
4. Post-copulation--Type A phonatomes similar to those of disturbance, but up to 0.5 sec long, 25 1/2°C.

5. Post-copulation--Type D sounds.

6. Post-copulation--Type E sounds.

7. Strong Aggression (Male agressor)--Type C phonatomes with 3 to 14 bars. Phonatome length up to 0.39 sec at 24 1/2°C.

8. Strong Aggression (female aggressor)--Type B phonatomes about 0.02 sec at 26°C.

9. Strong Aggression (male and female aggressors)--Type E phonatomes.

10. Strong Aggression (aggressee)--Type A phonatomes similar to those of disturbance.

11. Mild Aggression--Type D sounds

12. Disturbance--Type A phonatomes 0.08 to 0.29 sec duration at 26°C.

13. Solo (feeding or inactive)--Type D sounds.

14. Solo (walking)--Type B phonatomes similar to female aggressive signal.

The only behavioral context not observed for *O. disjunctus* is the post-aggression pushups. The only sound types not observed were Type F, associated with pushups, and Type G associated with solo feeding. By adding to this the fact that some species produce sound types that are different from those of *O. disjunctus* in a given context, the total variety of signals produced by Passalidae is increased even more. Nor does this classification include signals produced in adult-larval or larval-larval interactions. Larval studies are as yet incomplete, but I have noted at least 1 larval sound type produced in a minimum of 3 behavioral contexts.

Alexander (1966) states that a cricket, *Anurogryllus 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 for 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 single species of arthropod.

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BIOGRAPHICAL SKETCH

Jack Clayton Schuster eclosed on 20 February 1944 in Dearborn, Michigan. In June 1962, his second stadium was terminated at Roseville High School, Roseville, Michigan As a third instar, he attended the University of Michigan where he received the degree of Bachelor of Sciences with a major in Biology and a Secondary School Teaching Certificate in April 1966. Here he entered a prepupal stage that terminated when the degree of Master of Science with a Biology major was conferred in April 1968. He pupated at the University of Florida. In no sense was this a "resting stage." His prepupal and pupal stadia were characterized by extreme vagility. His migrations included all countries of Central America and many of South America and the Caribbean. A period of diapause (1969-72) was spent at the Universidad Nacional Agraria de la Selva, Tingo Maria, Peru, as a visiting professor with the U.S. Peace Corps, before resuming pupal ontogeny at the University of Florida. His ghost-like, diaphanous exuvium was reportedly observed during nocturnal sojourns in the Gainesville area accompanied by a swarm of other minstrels stridulating at various pubs and laundromats while the diurnal pupa presented a visage, axe in hand, earphones covering the auditory tympana, listening to moldy logs while reclining in a mesic hammock. Sexual paedogenesis recently gave rise to a female first instar, Kalara Jean. After pupal ecdysis and the reception of the Doctor of Philosophy degree, the imago will be engaged in teaching and research at the Universidad del Valle, Guatemala City, Guatemala, with his wife Laura, a botanist.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas J. Walker, Chairman
Professor of Entomology
and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

James E. Lloyd
Professor of Entomology
and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

F. C. Johnson

F. C. Johnson
Professor of Zoology

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Reese I Sailer

Reese I. Sailer
Professor of Entomology
and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 1975

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