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ACOUSTIC BEHAVIOR OF FOUR SYMPATRIC SPECIES OF WATER SCAVENGER BEETLES (COLEOPTERA, HYDROPHILIDAE, *TROPISTERNUS*)

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INTRODUCTION

THE GENUS *Tropisternus* consists of 56 species and subspecies of water scavenger beetles restricted to the Western Hemisphere. In Michigan, larvae can be found during spring and summer, and adults throughout the year (Spangler, 1960). The four species studied here, *mixtus, nimbatus, glaber,* and *natator,* can be collected in the same sweep of a net in pond and stream edges near Ann Arbor, Washtenaw County, Michigan.

Young (1958) described the mating behavior common to several species of *Tropisternus* and asked the question: "Is the mating behavior of different species different enough to present barriers to interbreeding?" Spangler (1960) reported that both males and females of five species of *Tropisternus* produce "squeaking sounds," and that both a male and female of *ellipticus* were heard to squeak as the male "pursued" the female prior to copulation. Van Tassell (1965) figured audiospectrographs of both "stress" sounds and "premating" sounds of four species of another hydrophilid genus, *Berosus,* and suggested that premating sounds may be important as a reproductive isolating mechanism among sympatric species.

The four sympatric species of *Tropisternus* I studied produce sounds associated with their reproductive behavior. These sounds are distinctive for each species, and they may function to prevent interbreeding,

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although I have not demonstrated here that they do so. *Tropisternus* spp. produce sounds in five situations: 1) by isolated males or females or by individuals in groups when feeding or moving about under water with no known source of disturbance; 2) by sexually responsive males (males that mount other beetles contacted) when another individual is nearby but not yet mounted; 3) by males when mounted on the back of a male or female but not yet copulating; 4) by males or females when handled or otherwise disturbed; and 5) by previously inseminated females (of *mixtus* only) when a chirping male is close to or has mounted her. In situations 1) and 4), not all beetles always produce sounds. Sounds produced in the above situations are here designated, respectively, as calling (situation 1), courtship (situations 2 and 3), and disturbance (situation 4 and perhaps 5).

Calling signals are usually considered as signals that may be emitted in the absence of other individuals of the same species and bring about formation of a sexually responsive male-female pair by the attraction of either sex by the signal from the other; they may involve an exchange of signals between the male and female. Courtship signals are those which occur after pair formation and frequently culminate in copulation when the courted individual is sexually responsive (cf. Alexander, 1967).

This paper is the first detailed description of stridulation and associated behavior of species of *Tropisternus*. It shows that sound production is an integral part of the mating behavior of the four species described here, and that each species emits sounds which fit the calling, courtship, and disturbance signal categories of Alexander (1967).

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METHODS AND MATERIAL

Sounds were recorded in 1964–65 with a Magnemite Portable Tape Recorder, Model 610E, at a tape speed of 15 inches per second, using a D–33 American Dynamic Microphone. Playback for analysis was on a Magnecorder, Model PT63A2HZ, with a Magnecord Model PT63–J amplifier. In 1971 a Uher 4000 Report–L recorder was used at a tape speed of 7.5 inches per second along with a Sennhauser MD405S microphone. The same Uher was used for playback analysis. Rated frequency responses are 50–15,000 Hz (± 2 db.) for the Magnemite, 30–15,000 Hz for the D–33 microphone, 50–15,000 Hz for the Magnecorder, and 60–16,000 Hz for the Sennhauser microphone. The measured frequency response of the Uher is 50–10,000 Hz (± 3 db.) at 7.5 inches per second. Audiospectrographs were made with a Kay Electric Company Vibralyzer 7030A and a Kay Scale Magnifier 6076C set at upper and lower limits of 350 and 50. Sounds were played into the Vibralyzer at one-half the original tape speed with the Vibralyzer set at 80–8000 Hz. The settings for analyses were Wide Band Filter, Shape Flat, and Pattern Expanded. The Vibralyzer voltage unit level during recording and analysis was kept at –5 or below in all cases.

Recordings made in 1964–65 were obtained by covering the D–33 microphone with a condom and dipping it about one-fourth inch into the water. In 1971 the Sennhauser microphone was covered with an Alligator Baggie plastic bag and dipped about one-half inch into the water. Glass or plexiglass aquaria were used containing from one to two liters of water and aquatic vegetation. Plastic screen partitions divided the plexiglass aquaria so that male and female beetles could be kept separate while in the same acoustic and aquatic environment. Because the beetles were free to move about in the aquaria, the distance from microphone to stridulating beetles could not be controlled. Individuals were recorded one to five inches from the microphone. Rectangular containers were used for recording in preference to gallon jars, which produce echoes (Fig. 7b), but no other precautions were taken to reduce sound reflections. Individual beetles were isolated in either pint or gallon jars containing aquatic plants and pond edge debris. The jars were continually illuminated by either incandescent or fluorescent light. Water temperature in the jars varied from 60° to 80°F. under different conditions. Voucher specimens, audiospectrographs, and tape recordings are deposited in the Museum of Zoology of the University of Michigan, Ann Arbor, Michigan.

The micrographs of sound-producing structures were prepared using the University of Michigan JSM–U3 Scanning Electron Microscope. Two 100–200 Å coatings of gold were evaporated onto the samples, which were mounted on aluminum posts with silver paint. The samples were rotated 180° between coatings.

For words like frequency, pulse, and phrase, the acoustical terminology used here generally follows the glossary of terms in Alexander (1967). Subjective terms such as tick, chirp, buzz, and trill are assigned for ease and clarity in discussion. In general, ticks are single-pulsed sounds of less than 0.01 second duration; chirps are composed of a group of sound pulses so closely spaced in time that they are heard as a single sound; buzzes have pulses less closely spaced than chirps, but too close to be heard as distinct ticks; and trills are rhythmic trains of chirps (Fig. 1). A phrase is any group of low-pitched sounds, such as a group of ticks, or a group of chirps making up an unbroken trill. The disturbance chirps discussed here correspond to the "stress" chirps of Van Tassell (1965).

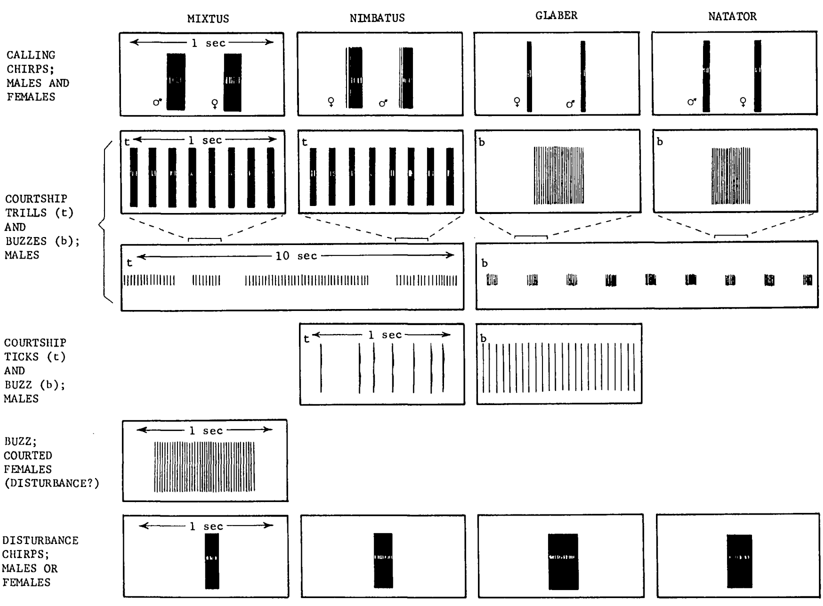

FIG. 1. Diagram comparing sounds produced by *Tropisternus mixtus, nimbatus, glaber,* and *natator*. Sounds are arranged vertically according to species and horizontally according to behavioral context. The third row expands the time scale for the courtship sounds shown in the second row to ten seconds (repetition rates are similar for *mixtus* and *nimbatus* trills, and for *glaber* and *natator* buzzes). All other diagrams represent one second durations.

SOUND PRODUCTION

Sounds produced by these species result from friction between a plectrum on each laterosternite of the first visible abdominal segment moved against a pars stridens on the underside of each elytron (Fig. 2). Simple experiments were performed to determine the location of the sound-producing structures. Excising the small parts of the elytra presumed to bear the partes stridentes, enameling the partes stridentes, or enameling the presumed plectra stopped sound production. Cutting off all the elytra posterior to the partes stridentes, excising sections of the elytra anterior to the partes stridentes, enameling the under surface of the elytra except for the partes stridentes, and removing the metathoracic wings did not prevent sound production.

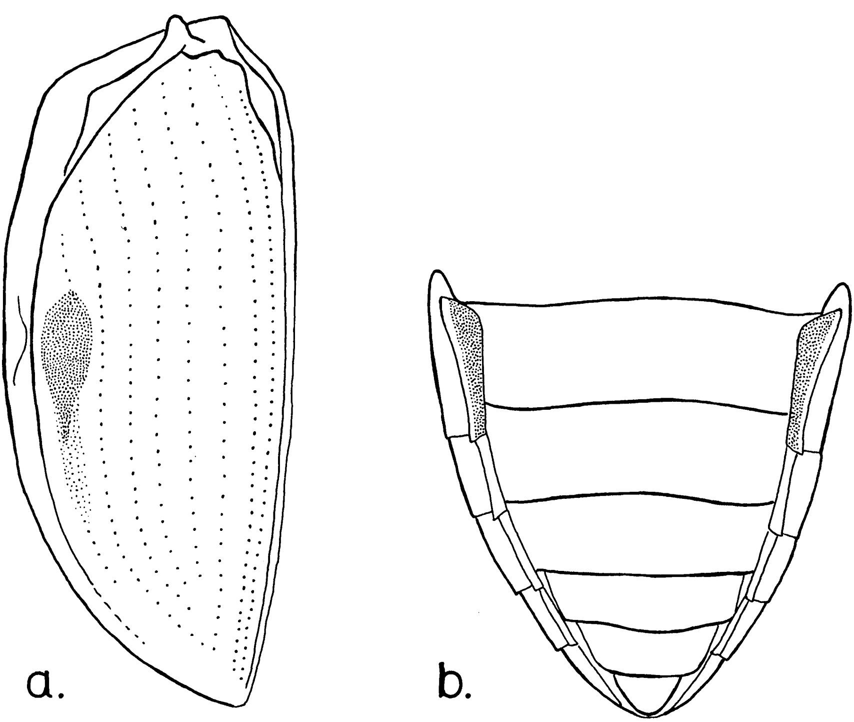

FIG. 2. Location of sound-producing structures of *Tropisternus mixtus:* (a) ventral view of right elytron with the pars stridens stippled, and (b) dorsal view of abdomen with both plectra stippled.

Stridulations appear to be accompanied by movement of the abdomen upward and forward against the elytra. Apparently no sounds are produced by the abdomen moving in the reverse direction. The metathoracic wings lie folded mediad to the plectral ridges of the laterosternites and do not prevent them from touching the elytra. No abdominal movement has yet been observed associated with the production of ticking sounds emitted by males of *nimbatus* (Fig. 1); however, a series of ticks may be produced by a very slow, single stroke of the abdomen, which would be difficult to detect in these small and freely-moving beetles.

The plectral surfaces of males of all four species are covered with very small, slightly curved, specialized setae pointing generally posteriorly; and the surface of each elytral pars stridens is covered with rows of tiny papillae (Fig. 3). Female stridulatory surfaces have not yet been studied by electron microscopy.

Chirps of all four species have relatively intense bands of frequencies between 1.0 and 4.5 kHz, with less intense frequencies both below and above this band; but these carrier frequencies may vary more than 1.0 kHz higher and 0.5 kHz lower than normal depending upon conditions. In general, as a chirper moves further from the microphone or closer to the surface, the higher frequency bands are recorded as most intense. Chirps of beetles with the posterior half of the elytra removed showed decreased amplitude and some loss of lower frequency bands, but remained within the same frequency range. Out of water, the carrier frequencies range from 1.0 to 2.0 kHz higher. Measurements of disturbance chirps of a single *mixtus* female at different water temperatures indicate that increasing temperature hardly affects the carrier frequencies but may decrease the average chirp duration (Table 1).

Although intensities have not been measured directly, chirps of *Tropisternus* in aquaria have been heard at a distance of 20 feet across a quiet room. All four species of *Tropisternus* stridulate in water

TABLE 1

DISTURBANCE CHIRPS OF ONE *Tropisternus mixtus* FEMALE AT THREE TEMPERATURES

Temperature (degrees F.)	Ave. duration (seconds)	Range (seconds)	Ave. carrier freq. (kHz.)	Number of chirps
100	0.06	0.05–0.07	1.0–3.0	17
80	0.10	0.08–0.11	1.0–3.0	8
65	0.12	0.06–0.14	1.0–3.0	5

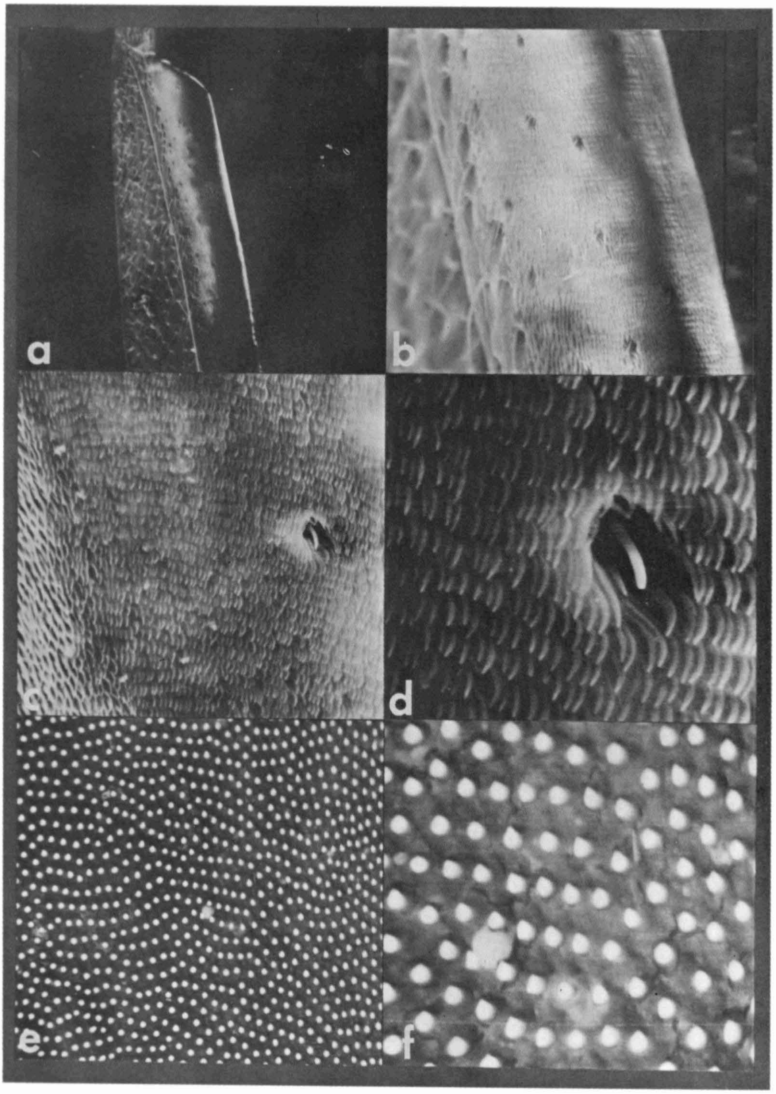

FIG. 3. Scanning electron micrographs of stridulatory surfaces of males of *Tropisternus*, top of each micrograph oriented anteriorly. (a) *mixtus:* dorsal view of plectrum on ridge of left laterosternite (light area), abdominal tergites to right of ridge (dark area) (X100); (b) *mixtus:* same plectrum (X500); (c) *nimbatus:* dorsal view of left plectrum (X1000); (d) *nimbatus:* same plectrum (X3000); (e) *mixtus:* ventral view of pars stridens on right elytron (X1000); (f) *mixtus:* same pars stridens (X3000).

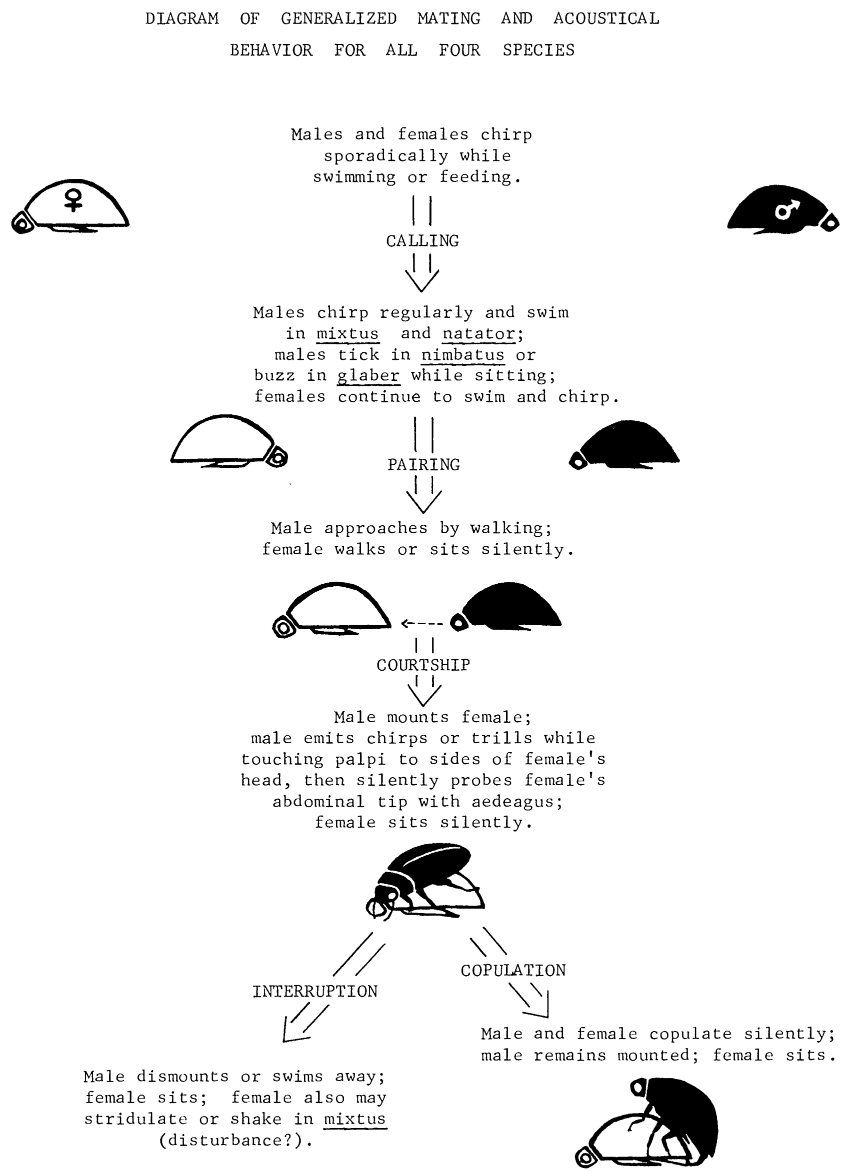

FIG. 4. Diagram of generalized mating and acoustical behavior of four species of *Tropisternus*.

rather than on the water surface, although they often chirp just beneath the surface. However, disturbance chirps may be produced both in and out of water.

MATING BEHAVIOR

The general aspects of the mating behavior of all four species are similar enough to be described together (Fig. 4). Young (1958) has already published an excellent account of the mating behavior of *Tropisternus* species from observations of *nimbatus, natator,* and *striolatus,* to which can now be added the role of acoustical behavior and some other details. Often a beetle will orient toward, approach, and touch its palpi to another beetle located within one or two cm. The approaching beetle may move to the head and touch its palpi to the other's palpi before moving away. Both beetles remain silent in this type of encounter. Males and females approach other beetles irrespective of the sex or species of *Tropisternus* approached. Many males that have been isolated from other individuals in the laboratory are silent unless disturbed; however, all males observed to mount other individuals chirped sporadically while isolated earlier the same day. Although sexually responsive males chirp, some males which did not mount other individuals contacted also were heard chirping.

A sexually responsive male turns toward any male or female within about 1 cm (apparently orienting visually) and generally in front of him. He moves to the other beetle, mounts its back, often without any observable preliminaries, walks forward, and touches his palpi to the end of the mounted beetle. If he mounts head to tail, his palpi touch the tip of the abdomen, and he then turns around and moves to the head. Depending on the species, a sexually responsive male emits courtship stridulations either as he approaches and mounts or after mounting the other individual (Figs. 1, 4). Courtship stridulations are produced by mounting males regardless of the sex of the mounted beetle. While stridulating, the male touches his palpi (and antennae ?) to one side of the head of the mounted beetle, moves his palpi rapidly, and then shifts over to the other side of the head. After repeating this shift from one side of the head to the other side several times, the male either steps backward and probes the female's genital area with his extended aedeagus or swims away. If probing does not quickly lead to copulation, the male either moves forward and begins touching the sides of the head with his palpi again or swims away. Male courtship stridulation while mounted occurs only during the head-touching behavior. Males fall silent when moving back to probe and are silent during copulation.

Following the introduction of a chirping female into an aquarium with a chirping male *nimbatus* or *glaber,* the male eventually stops swimming, stops producing calling chirps, and begins producing species–characteristic sounds, ticks in *nimbatus* and buzzes one to two seconds long in *glaber*. Because they are produced only in the presence of another beetle, ticks and long buzzes seem to be a second type of courtship sound. Ticking *nimbatus* males and buzzing *glaber* males mount any individual moving into apparent visual range and begin mounted courtship sounds, which are distinct from sounds emitted prior to physical contact (Fig. 1).

Chirping females of *mixtus, nimbatus,* and *glaber* continue to chirp and swim from place to place in the presence of a chirping male of the same species, but stop swimming and fall silent when mounted by a male. Females typically sit quietly during mounting, probing, and copulating. Sexually receptive *natator* females were not collected at the same time as males, and their response to chirping *natator* males is not known. Only a few females of one species, *mixtus,* have been heard stridulating when mounted by males (Fig. 5g). These females did not copulate but did lay viable eggs within a few days, indicating prior insemination. Mounted females sometimes hold their rear legs horizontally behind them, cross the tibiae, wipe them together in scissor-like fashion, and contact the male's aedeagus as he probes. Males touched this way while probing retract their aedeagus and move forward to the head again, or dismount.

Females deposit their eggs in cases that they construct under water using silk from spinnerets located near the tip of the abdomen. Egg cases are generally fastened to vegetation or debris near the water surface. Clutches of 5–23 eggs were deposited in egg cases by seven *mixtus* and four *nimbatus* females, three or four days after copulation. The predaceous larvae emerge after four or five days at room temperature in aquaria and capture small aquatic arthropods, or sibling larvae, which they hold above the water surface with their mandibles and consume, discarding the exoskeletons.

Tropisternus mixtus (LeConte)

Calling chirps and disturbance chirps are similar in frequency and duration, and also similar in males and females (Table 2) (Figs. 5a, 5e, 6a). When isolated, the beetles commonly cling to and browse on the vegetation, and they either emit single chirps every two or three

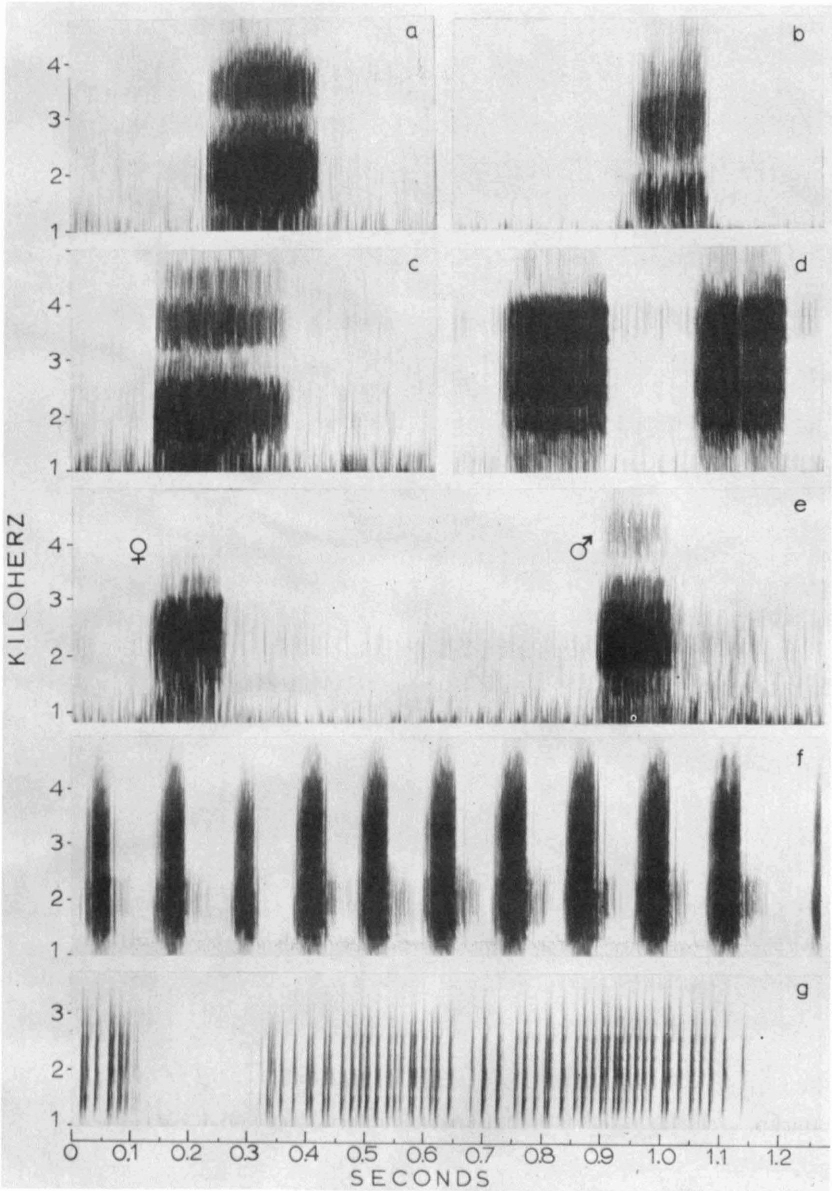

FIG. 5. Audiospectrographs of sounds of *Tropisternus*. Disturbance sounds of males: (a) *mixtus*, (b) *nimbatus*, (c) *glaber*, and (d) *natator*. Sounds of *mixtus*: (e) calling chirps of male and female, (f) courtship trill of mounted male, and (g) buzz emitted by female when approached or mounted by chirping male.

minutes or are silent. A male and female that had been isolated for several days and heard chirping were transferred on June 22, 1971 into opposite sides of a screen-divided aquarium. Their chirp rates increased from less than one chirp per minute to 12.5 and 9.5 chirps per minute respectively (in 1.7 minutes measured) after a few minutes. A minute or two after the screen was removed, the male sighted the female, moved to her, mounted her immediately, and began trilling (Fig. 5f). The trills ranged from two to 65 successive chirps with pauses of less than one-half second to eight seconds. A succession of 19 trills was followed by silence for 26 seconds while copulation occurred. Jarring the aquarium seemed to interrupt copulation; and the male trilled three more times, was silent for 12 seconds more of apparent copulation, and then released the female. The female was isolated and spun an egg case after four days. The egg case was found to contain four active and 16 not yet fully developed larvae after five days.

Only four copulations were tape recorded. They ranged from 50 seconds to three minutes (average, two minutes) from the time the male mounted until he released the female. All four of these copulating females remained silent. Four other females produced a distinctive buzz (Fig. 5g) when approached or mounted by chirping males during nine encounters observed. Males courting these buzzing females either turned and walked or swam away from them without mounting, or dismounted from the female without copulating. All four females showing this behavior laid eggs within 3–5 days. One of these four females was again mounted by a male 18 days after egg-laying, following 21 days of isolation from other beetles. Although she was silent while

TABLE 2
Tropisternus mixtus. SOUND MEASUREMENTS BETWEEN 70° AND 80°F.

Type of stridulation	Average (seconds)	Range (seconds)	Sample size	Source
Calling				
Chirp duration	0.18	0.11–0.22	37 chirps	4♂, 4♀
Courtship				
Trill chirp duration	0.05	0.03–0.07	77 chirps	6♂
Trill rate (chirps)	7.8/	5.0–9.0/	132 chirps	9♂
Trill duration	1.4	0.05–55.00	100 trills	9♂
Disturbance				
Chirp duration	0.14	0.08–0.20	38 chirps	2♂, 3♀
Buzz duration	0.6	0.3–0.9	7 buzzes	4♀
Buzz pulse rate (pulses)	93./	62.–168./	7 buzzes	4♀

he mounted, she touched his aedeagus with her hind legs each time he probed, and copulation did not occur.

Males were observed mounting other males eight times; each mounting male released the other after 10–80 seconds (average 30 seconds). In every case, the acoustical and other behavior appeared similar to that of males when courting females. One male stridulated repeatedly while mounted by another male, but the other seven males were silent while mounted.

Tropisternus nimbatus (Say)

When isolated or placed together in an aquarium, *nimbatus* males and females either were silent or produced calling chirps (Fig. 6e) that were shorter in average duration than their disturbance sounds (Figs. 5b, 6b) (Table 3). Although isolated males and females were heard to chirp sporadically a few times per minute, their chirp rates were not tape-recorded or measured. In one observation at 78°F., a male and female placed together produced 50 chirps in the first minute and 48 chirps in the next one-half minute. Then the male ceased chirping and began ticking (Fig. 6f) while the female emitted 36 chirps in the next one-half minute. The male remained in one location while ticking, and the female swam rapidly about the aquarium while chirping, pausing on vegetation only a few seconds at a time. In an observation of a chirping male and female that were separated by a wire screen, the male moved to the screen, remained there, and began tick-

TABLE 3

Tropisternus nimbatus. SOUND MEASUREMENTS BETWEEN 73° AND 78°F.

Type of stridulation	Average (seconds)	Range (seconds)	Sample size	Source
Calling				
Chirp duration	0.08	0.05–0.14	44 chirps	4♂, 1♀
Courtship				
Tick phrase duration	0.84	0.63–1.12	9 phrases	3♂
Tick phrase rate (phrases)	0.15/	0.08–0.23/	45 phrases	4♂
Tick rate (pulses)	8.2/	6.0–12.0/	9 phrases	3♂
Trill chirp duration	0.04	0.03–0.09	33 chirps	4♂
Trill rate (chirps)	8.3/	7.0–9.0/	166 chirps	4♂
Trill duration	1.9	0.5–5.5	14 trills	4♂
Disturbance				
Chirp duration	0.10	0.05–0.13	81 chirps	3♂, 2♀

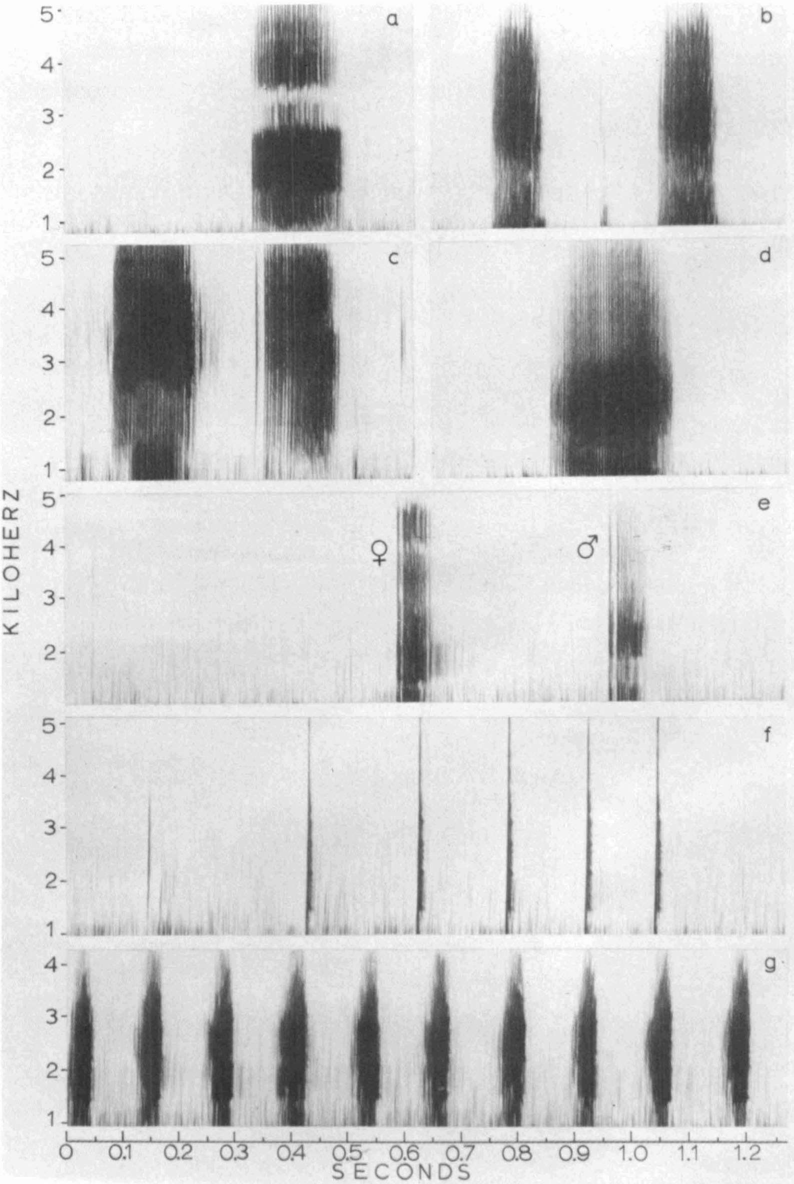

FIG. 6. Audiospectrographs of sounds of *Tropisternus*. Disturbance sounds of females: (a) *mixtus,* (b) *nimbatus,* (c) *glaber,* and (d) *natator*. Sounds of *nimbatus:* (e) calling chirps of male and female, (f) courtship ticks of male, and (g) courtship trill of mounted male.

ing. The female chirped continuously while swimming rapidly about the aquarium, and then settled on the screen and walked to the male. Both remained at the same location but on opposite sides of the screen, the female chirping and the male ticking, until they were removed after five minutes.

In other observations, five male–female mounting sequences were recorded, one ending with copulation. A ticking male turning and moving toward another male or female within about 1 cm begins a trill (Fig. 6g) similar to the trill of a male of *mixtus* (Fig. 5f). Trills of 4–40 shortened chirps (average, 15 chirps; sample, 14 trills), separated by pauses of varying duration, continued during mounting and until the genitalia were engaged or until the beetles separated without copulating.

Tropisternus glaber (Herbst)

The acoustical and reproductive behavior of *glaber* is known only from interactions of two males and one female, and a single observation of pair formation and copulation on May 6, 1965. The isolated male and female produced calling chirps (Fig. 7d) of similar frequency and shorter duration than their disturbance chirps (Figs. 5a, 6a) (Table 4). The female produced 3.5 chirps per minute (range 0–10 chirps per minute) in a five minute period. When placed together, the male and female combined chirped 23 times in the first two minutes, after which the male emitted buzzes of 1–2 seconds duration (Fig. 7e). Female chirping increased from 11 chirps during the first minute of male buzzing to 37 and 25 chirps in the ensuing two minutes. The male then contacted the female, mounted, and emitted a series of short

TABLE 4

Tropisternus glaber. SOUND MEASUREMENTS BETWEEN 70° AND 80°F.

Type of stridulation	Average (seconds)	Range (seconds)	Sample size	Source
Calling				
Chirp duration	0.02	0.02–0.03	30 chirps	2♂, 1♀
Courtship				
Long buzz duration	1.50	1.05–1.90	35 buzzes	2♂
Long buzz rate (buzzes)	0.35/	0.30–0.40/	52 buzzes	2♂
Long buzz pulse rate (pulses)	28./	18.–38./	21 buzzes	2♂
Short buzz duration	0.30	0.13–0.45	12 buzzes	1♂
Short buzz rate (buzzes)	1.13/	....	17 buzzes	1♂
Short buzz pulse rate (pulses)	93./	68.–109./	12 buzzes	1♂
Disturbance				
Chirp duration	0.17	0.10–0.24	31 chirps	1♂, 1♀

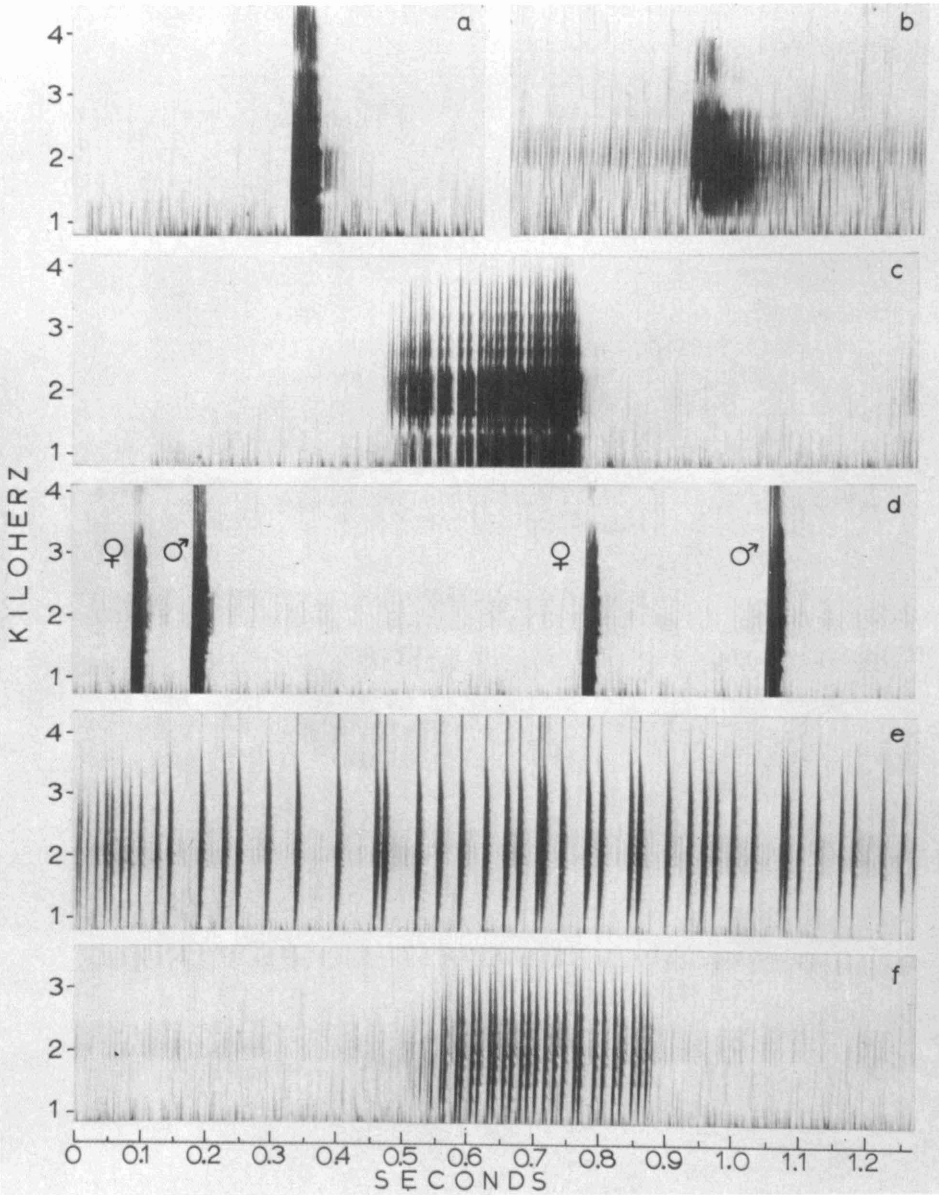

FIG. 7. Audiospectrographs of sounds of *Tropisternus*. Sounds of *natator:* (a) calling chirp of male, (b) calling chirp of female, (c) rhythmically repeated courtship buzz of mounted male. Sounds of *glaber:* (d) calling chirps of male and female, (e) long courtship buzz of male, and (f) rhythmically repeated, short courtship buzz of mounted male.

(about 0.3 second), rhythmic buzzes (Fig. 7f). The female was silent and apparently motionless while mounted.

Tropisternus natator (D'Orchymont)

The calling chirps produced by isolated *natator* males and females (Figs. 7a, 7b) were of shorter duration than disturbance chirps (Figs. 5d, 6d) and similar to *glaber* chirps (Fig. 7d) in frequency and duration. The slight difference in average disturbance chirp duration of males and females may be due to small sample size (Table 5). In the audiospectrograph of a calling chirp of a female of *natator* isolated in a glass gallon jar (Fig. 7b), the chirp consists only of the 0.04 second of the sound that has frequencies ranging up to four kHz; the additional 0.06 second of sound following the chirp at frequencies below three kHz is a ringing sound set up in the glass jar by the calling chirp.

TABLE 5

Tropisternus natator. Sound Measurements Between 73° and 76°F.

Type of stridulation	Average (seconds)	Range (seconds)	Sample size	Source
Calling				
Chirp duration	0.04	0.03–0.05	20 chirps	1 ♂, 1 ♀
Courtship				
Buzz duration	0.22	0.16–0.31	20 chirps	1 ♂
Buzz rate (buzzes)	1.17/	1.13–1.18/	210 buzzes	1 ♂
Buzz pulse rate (pulses)	97./	84.–110./	20 chirps	1 ♂
Disturbance				
Chirp duration	0.16	0.07–0.20	22 chirps	2 ♂
Chirp duration	0.19	0.15–0.24	28 chirps	2 ♀

The only male observed to pair with a silent female did not copulate with her. The male chirped 15 times in one minute before he came within 1 cm of the female and then began to buzz rhythmically (Figs. 1, 7c). The rhythmic buzzes continued as the male mounted the female and performed palpal-touching and genital-probing behavior similar to the other species of *Tropisternus*. After dismounting without copulating, the male continued to chirp. Four mountings by this male on July 2–3, 1971, lasted 15–125 seconds (average 82 seconds). A female collected and isolated May 3, 1965, emitted chirps similar in frequency and duration to male chirps; however, no male was available to place with her. On July 15, 1971, a silent male and female placed together contacted each other repeatedly without the male mounting.

DISCUSSION

Comparison of the sounds of species of *Tropisternus* (Fig. 1) shows structural similarities and differences, principally in their calling and courtship sounds. Males of *mixtus* change from isolated calling chirps to rapid successions of shortened courtship chirps (trills). Males of *glaber* and *natator* change from calling chirps to courtship buzzes, lengthening chirp duration. *Tropisternus glaber* produces initial courtship buzzes of one to two seconds duration before mounting and changing to the rhythmic, shorter, courtship buzzes similar to those of *natator*. Males of *nimbatus* change from chirps to initial courtship ticks, lengthening the calling chirp and producing single pulses, heard as separate ticks. After mounting, males of *nimbatus* produce rapid successions of chirps similar to shortened calling chirps. Females of *mixtus* sometimes buzz when courted by males; these buzzes are longer but otherwise similar to calling chirps.

Experiments have not been performed to demonstrate the functions of the sounds produced by any species of *Tropisternus,* or any aquatic beetle, for that matter. However, excluding disturbance chirps, the chirps, ticks, buzzes, and trills of males, and the chirps and buzzes of females of these species of *Tropisternus* are closely associated with mating behavior and likely candidates for calling and courtship functions.

Stridulations produced by males of all four species of *Tropisternus* when mounting females seem to fit the courtship category perfectly. The ticks of males of *nimbatus* and the long buzzes of males of *glaber,* which were never emitted by isolated beetles and which always preceded mounting behavior, also fit the courtship category. It is not known if any of these courtship sounds are essential for copulation.

The chirps emitted by males and females in isolation fit the calling category reasonably well. Especially in *mixtus* and *nimbatus,* these chirps appear to stimulate an increase in chirp rate and locomotory activity in conspecific individuals located nearby but apparently beyond the range of visual or tactual stimuli. Of course, chemical signals and the consequent reinterpretation of observations are not ruled out, but chemical signals between hydrophilid beetles have not yet been reported or suggested.

Alexander, Moore, and Woodruff (1963) hypothesized that in any closely related species of sound-producing beetles living close together in restricted niches, disturbance sounds would be expected to remain non-specific, but courtship and congregational signals should evolve greater specificity. Comparison of the disturbance sounds of these four species (Figs. 1, 5a–d, 6a–d) shows that very few structural differences exist between them. By contrast, the sounds which regularly occur prior to mating among the four species are distinct for each species. It remains to be established whether or not any of the sounds regularly produced in calling or courtship situations by these species, or by other hydrophilid beetles, is essential for mating, acts as a primary congregating mechanism, or is a primary isolating mechanism, reducing the likelihood of interspecific mating.

LITERATURE CITED

ALEXANDER, R. D. 1967. Acoustical communication in arthropods. A. Rev. Ent., 12:495–526.

ALEXANDER, R. D., T. E. MOORE, AND R. E. WOODRUFF. 1963. The evolutionary differentiation of stridulatory signals in beetles. Anim. Behav., 11:111–115.

DUMORTIER, B. 1963. Morphology of sound emission apparatus in arthropods. *In:* Busnel, R. G. (ed.). Acoustic behaviour of animals. New York: Elsevier Publ. Co., xx + 933 pp.

SPANGLER, P. J. 1960. A revision of the genus *Tropisternus* (Coleoptera: Hydrophilidae). Ph.D. Dissertation, University of Missouri, 365 pp.

VAN TASSELL, E. R. 1965. An audiospectrographic study of stridulation as an isolating mechanism in the genus *Berosus* (Coleoptera: Hydrophilidae). Ann. ent. Soc. Am., 58(4):407–413.

YOUNG, F. N. 1958. Notes on the care and rearing of *Tropisternus* in the laboratory (Coleoptera: Hydrophilidae). Ecology, 39(1):166–167.