

Rovner, J. S. 1980. Vibration in *Heteropoda venatoria* (Sparassidae): A third method of sound production in spiders. *J. Arachnol.*, 8: 193-200.

VIBRATION IN *HETEROPODA VENATORIA* (SPARASSIDAE): A THIRD METHOD OF SOUND PRODUCTION IN SPIDERS¹

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ABSTRACT

Pheromone-stimulated male *Heteropoda venatoria* (L.) produce sounds during bouts of leg oscillations while coupled to the substratum by their tarsal adhesive hairs. No stridulatory organ is involved. Preventing palpal percussion and abdominal vibration does not eliminate primary sound production. Leg oscillation rates of 63, 83, and 125 Hz, roughly estimated from high-speed cinematographic samples of signalling, were within 1 SD of the mean frequencies of the lowest ($\bar{Y} = 88$ Hz) or highest ($\bar{Y} = 146$ Hz) frequency wave-trains, as indicated by oscillographic analysis of such sounds. These signals resemble and are analogous in origin to insect flight-sounds, the fundamental frequency being determined directly by the appendage oscillation rate. Hypotheses about the roles of vibration in these and other spiders, including araneids, are considered.

INTRODUCTION

Sound production in spiders usually involves stridulatory organs or, less frequently, percussion (Legendre 1963; Rovner 1975). We now can add to stridulation and percussion a third method of sound production, one which is analogous to the generation of flight-sounds in insects. During pre-copulatory bouts of vibration males of the nocturnal, long-legged, wandering spider *Heteropoda venatoria* (L.) produce a sound faintly audible to the unaided human ear as a low-frequency "buzz" or "hum".

METHODS

In late June, 1978, I collected penultimate and adult *H. venatoria* at night in an avocado (*Persea americana*) orchard at the University of Florida's Agricultural Research and Education Center in Homestead, Florida. After being transported to my laboratory in Ohio, the spiders were maintained in their individual cages with a constant water supply and weekly feedings of crickets (*Acheta domesticus*) and, occasionally, large dipterans.

¹ This study was supported by NSF grant BNS 76-15009.

All the immature spiders reached adulthood by mid-July. Adult males had a body length of 17 mm. I observed reproductive behavior in the late evening (usually between 2100 and 2300 hr) during July-October. Temperatures ranged from 17 to 22°C.

For each recording or filming session, I introduced one of three males to a vacant glass cage (terrarium or battery jar) that had just been occupied by a female conspecific. To record the air-borne components of the signal, I used a PML condenser microphone (Model DC-21) suspended about 5 cm above a horizontal substratum of dead avocado leaves. (When collected, most of the spiders were observed resting on such dried leaves beneath the trees or on the living leaves of the lower branches of the trees.) To record the substratum-borne component of the sound, I attached a high-sensitivity vibration pickup (General Radio, Type 1560-P14) to a vertical cardboard substratum. Oscillograms were obtained with a Tektronix oscilloscope (Model D44) and a Grass kymograph camera (Model C4) running at 100 or 25 mm/sec. Sonographic analyses involved use of a Voice Identification Inc. sound spectrograph (Series 700). Portions of courtship were filmed with a Cine-8 Super 8mm camera (Visual Instrumentation, Model SP-1) at 250 frames/sec.

To determine experimentally whether palpal contact with the substratum is essential for sound production, as usually is true in another family of wanderers, the lycosid spiders, I placed both palps of one male in a paraffin-fixed, human hair sling above the anterior cephalothorax (see Rovner and Wright 1975 for technique). To prevent abdominal oscillations, I attached the abdomen of this same male to the cephalothorax with a paraffin bridge. Both operations involved CO₂ anesthesia. In this paper, means are accompanied by S.D.'s.

RESULTS

Courtship Behavior.—After introduction to the female's vacated cage, the male wandered over the walls, ceiling, and floor. He alternated bouts of palpal exploratory behavior with longer periods in which he was stationary. At the latter times, the tarsi of all of the widely spread legs were fixed to the vertical or horizontal substratum and the body partly elevated (Fig. 1). While in this rigid position, the male performed bouts of vibration, during parts of which, buzzing or humming sounds could be heard by the unaided ear up to at least 0.3 m away, even when the spider was on glass. Downward jerks of the body, each accompanied by a single caudal palpal scrape, occurred at intervals. Very brief, broad-spectrum noises sometimes were coincident with these body jerks.

Oscillographic Analyses.—Sound production resulting from appendage oscillations involved a series of intermittent, very low amplitude "minor" wave-trains that culminated in a louder primary signal lasting approx. 2.5-4.0 sec (Figs. 2 and 3). The primary signal usually contained four distinct wave-trains. It began with several (3.8 ± 2.62 , $n = 25$) closely spaced, brief wave-trains that I termed "pre-majors," which usually showed successive increases in amplitude. These typically were followed by a longer, two-part wave-train, "major, A and B", that had higher frequencies and relatively homogeneous waves. High-amplitude waves were characteristic of the major A wave-train, while those of the major B could be of either lower or higher amplitude than the major A. (During bouts of low intensity courtship, the major A and B wave-trains were not as distinctive as those in Figs. 2 and 3.) The final portion of the primary signal was of lower amplitude than the

major but contained the highest frequencies in its several wave-trains called “post-majors”. Thus, the primary signal of untreated males showed a trend of increasing frequencies in successive wave-trains (Table 1). This increase in pitch as each primary signal progressed toward its end point was readily audible to the human ear.

Two-tailed *t*-tests were used here and later to test the hypothesis that there was no difference between the mean frequencies of each type of wave-train for those samples having similar variances. In the case of the untreated males, the post-major wave-train had a higher frequency than the pre-major ($t = 10.63, P < 0.001$). Likewise, the major B wave-train had a higher frequency than the preceding major A wave-train ($t = 6.87, P < 0.001$).

After the primary signal ended, an inactive period or a bout of exploratory behavior often occurred during a relatively quiet period lasting 36.7 ± 19.60 sec ($n = 30$). Then there was a series of very low amplitude minor wave-trains during a variable interval lasting 28.8 ± 21.74 sec ($n = 28$), this series giving way to another primary signal. Thus, the pattern of courtship signalling in male *H. venatoria* is an alternation of a relatively quiet period that includes low-level sound-bursts with a period consisting of the louder primary signal.

As shown in the sample oscillograms (Figs. 2 and 3), most of the acoustic signal consists of relatively simple, often sinusoidal-like waveforms. This suggests that little energy is present as harmonics above the fundamental frequencies. The sonographic analyses supported this interpretation, harmonics of the vibration-generated fundamental frequency being present only in certain parts of the signal and not extending above about 800 Hz.

Signalling by the Treated Male.—Neither preventing palpal contact with the substratum nor preventing abdominal oscillations resulted in a loss of sound production in the male so treated. There was no difference between this male and the untreated ones as to the frequencies of the pre-major ($t = 0.85, NS$) or post-major ($t = 1.40, NS$) wave-trains.

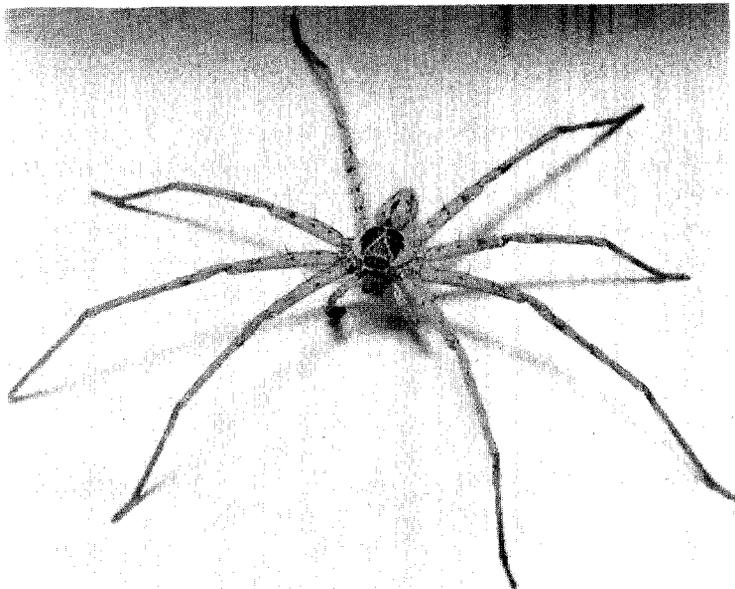


Fig. 1.—*Heteropoda venatoria* in the courtship posture on the wall of a cage (approx. 1.4 X). The camera was aimed obliquely upward.

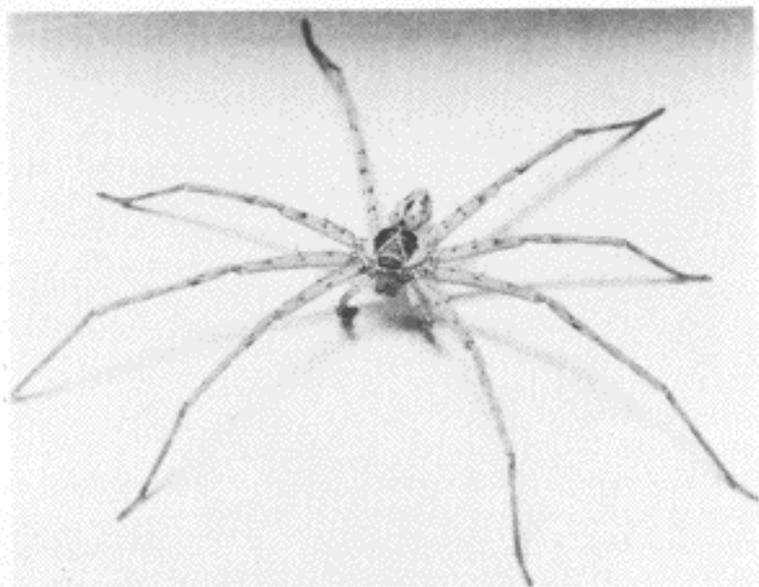


Fig. 1.—*Heteropoda venatoria* in the courtship posture on the wall of a cage (approx. 1.4 X). The camera was aimed obliquely upward.

Within the signal of the treated male, the typical increase in frequency between the pre- and post-major wave-trains occurred ($t = 4.56, P < 0.001$). However, the major wave-train frequencies of the treated male were lower than in the untreated males (major A: $t = 6.75, P < 0.001$; major B: $t = 6.36, P < 0.001$) and the form of the signal was altered (Fig. 3). In another experiment a male lacking legs I produced sounds like those of intact males.

Cinematographic Analyses.—Slow-motion and frame-by-frame analyses of filmed samples of behavior in courting male *H. venatoria* revealed low-amplitude, vertical oscillations of the posterior pairs of legs and the abdomen. At times, leg oscillations involved only legs IV. Two, three, or four frames of film were required for completion of each oscillation, depending on the portion of courtship or the intensity of courtship being sampled. Thus, some sections of the films contained a series of 2-frame oscillations; others, 3-frame; yet others, 4-frame. At a camera speed of 250 frames/sec., these represent vibration rates of roughly 125, 83, and 63 Hz respectively. The highest rate of oscillation, 125 Hz, occurred in legs IV. These filmed oscillation rates fell within 1 SD of the mean frequencies of either the lowest or the highest frequency wave-trains obtained in the oscillograms of the primary signals (Table 1).

Slow-motion analyses also revealed that the body jerks occurring at intervals during courtship involved ventro-caudad dips of the body during which the palps were swept caudad from their otherwise stationary position. The body movements were derived from sudden changes in the degree of flexure of the proximal joints of the legs, especially the posterior pairs. Dips were 0.04 sec in duration. The interval from the onset of one dip to the onset of the next averaged 0.15 ± 0.03 sec ($n = 15$). This was similar to the interval between onsets of minor wave-trains (0.20 ± 0.07 sec; $n = 22$) in one of the oscillograms. An additional behavior revealed in one male that was filmed was a rapid waving of legs II during part of the intense vibration that occurs during primary signal production.

DISCUSSION

Mechanism of Sound Production.—Although courting male *H. venatoria* produce occasional noises percussively when body jerks occur, most of their acoustic signal is generated without the mechanisms known to function in other spiders—stridulation and percussion. The similarity of values for leg oscillation rates (determined cinematographically from samples of this behavior) and the fundamental frequencies of the primary signals (determined oscillographically from other samples of this behavior) suggests that *H. venatoria* produces humming sounds the same way that many winged

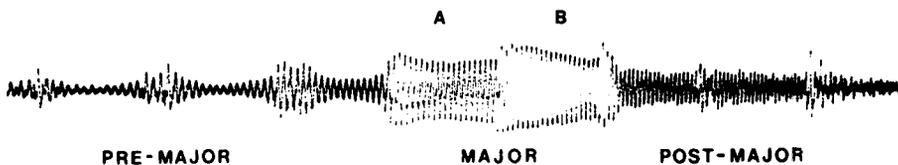


Fig. 2.—Oscillogram illustrating the wave-train components of the primary signal of courting male *Heteropoda venatoria*. Several “pre-major” wave-trains give way to a two-part “major” wave-train, which is followed by several “post-major” wave-trains containing the highest frequency sounds.

insects do, by the tuning fork-like effect of appendage vibrations that set up regions of compression and rarefaction (Haskell 1961).

The films suggest that vibration of the posterior legs, especially legs IV, are of major importance in generating the primary signal. Neither the palps nor the abdomen play a role in producing the fundamental frequency of this sound. Indeed, the abdominal vibrations during sound production in this species may be a purely passive, induced movement—a by-product of the leg oscillations.

Vibration in Other Arthropods.—*H. venatoria* has wave-trains that are within the range of the flight-sounds of certain coleopterans (75-100 Hz) and, in its upper range of pitches, overlaps the flight-sounds of some familiar hymenopterans (*Bombus* sp., 150 Hz) and dipterans (*Musca domestica*, 150-200 Hz) (Sotavalta 1963). Even when not flying, sound generation by appendage vibration occurs in insects: “piping” by holding the wings and thorax in a state of fine tremor in queen honeybees (*Apis mellifera*), and “singing” by vibrating only the wing bases in syrphid flies resting between flights (ibid.). The low, humming sound produced by vibration of the flexed large cheliped in male fiddler crabs (*Uca pugilator*) provides an example of this type of sound production in yet another class of arthropods (Burkenroad 1947). Although common in flying insects, such sound production by appendage vibration is otherwise rare in this phylum (Dumortier 1963), *H. venatoria* now being added to the few wingless arthropods using this mode.

Factors Affecting the Sounds.—As in the insects and crustaceans, resonance of the spider’s body or appendages, friction at joints, or other factors sometimes add harmonics to the fundamental frequency, thereby producing the more complex wave-forms that

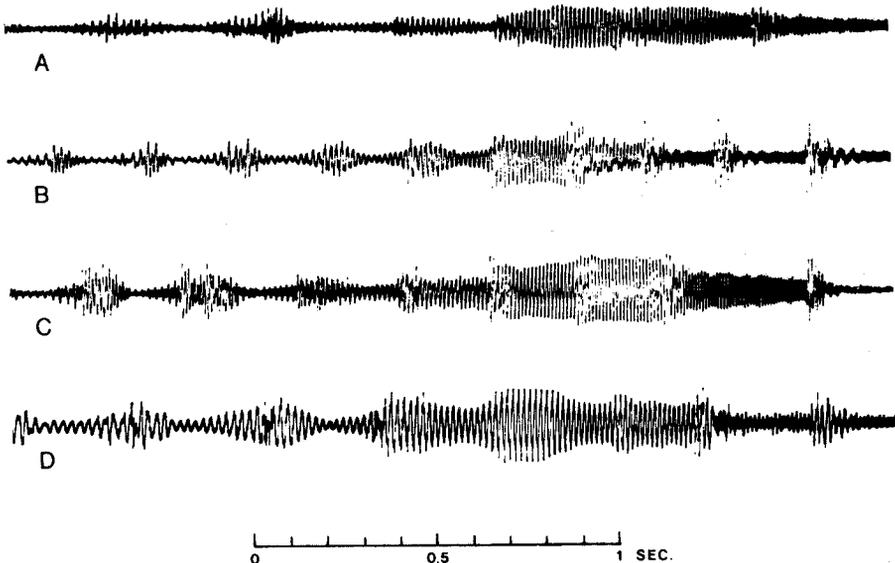


Fig. 3.—Oscillograms of primary signals of courting male *Heteropoda venatoria* arranged with the onsets of the major wave-trains lined up vertically (just to the right of center). (A) Airborne sound transduced by a condenser microphone; substratum of dried leaves. (B-D) Solid-borne sounds transduced by a vibration pickup; cardboard substratum. A, B and C were recorded from untreated males, while D was from a male with its palps in a paraffin-fixed sling and its abdomen attached with paraffin to its cephalothrax.

Table 1.—Mean frequencies (Hz) of wave-trains in courting male *Heteropoda venatoria*. (See Fig. 2).

	Pre-major	Major A	Major B	Post-major
Untreated Spiders	87.5 ± 24.76 (n=40)	93.7 ± 5.16 (n=15)	108.3 ± 6.45 (n=15)	145.7 ± 19.46 (n=30)
Treated Spider	81.0 ± 26.40 (n=15)	71.3 ± 8.54 (n=4)	83.8 ± 8.54 (n=4)	134.0 ± 31.43 (n=10)

occur at various points in the signal. In another regard, adding paraffin to parts of the body surface (and attaching major body parts to each other) changes the dynamics of the oscillatory movement. It has an effect similar to that caused by loading insect wings with collodion, which lowers the wingbeat frequency (Sotavalta 1963). This probably accounts for the reduced fundamental frequencies of the wave-trains produced by the male *H. venatoria* that was treated to prevent palpal percussion and abdominal vibration.

Importance of Substratum Coupling.—The attachment of *H. venatoria* to the substratum by the well-developed adhesive hairs of the claw tufts (Homann, 1957) is important in the effectiveness of this species' method of acoustic communication. The tetanic-like oscillations appear to involve considerable force. Were the posterior leg tarsi to slip on the substratum, the output of the mechanism generating the primary signal would be diminished. Furthermore, due to the spider's high sensitivity to solid-borne vibrations, it is likely that the substratum is the best medium for signal transmission. Playback experiments in lycosids indicated that substratum-conducted courtship sounds yielded stronger, more oriented responses from females than did airborne (Rovner 1967). Data obtained in the present study encourage me to put forth a generalization that sound production by wandering spiders always includes a substratum component, whether the mechanism be stridulation or percussion in lycosids (Rovner 1975; van Helssdingen personal communication), percussion in *Anyphaena accentuata* (Bristowe 1958), or vibration in *H. venatoria*.

Role of the Airborne Component.—Coupling to the substratum increases the loudness of the airborne acoustic component by incorporating the substratum into the system as a sounding-board. Based on the ability of lycosids to respond to airborne courtship sounds (Rovner 1967) and on the ability of *H. venatoria* to detect and capture insects that fly nearby (Rovner, unpublished data), it is likely that female *H. venatoria* receive the male's airborne sound by the single slit sensilla of the tarsi (Barth 1967), as well as use the trichobothria to detect air movements produced by the male's vibration (Görner and Andrews 1969). It probably is more than a coincidence that the male's signal involves frequencies like those of flying insects that are included in this species' diet. In spiders, the resolution and tuning of the primary sensory equipment for prey detection usually are adapted also for intra-specific communication.

Vibration in Other Sparassids.—The occurrence of acoustic signalling in *H. venatoria* suggests that future studies will reveal other sparassids to be using this mode of communication. Indeed, males of the Australian huntsman spider, *Isopoda immanis*, were described as having "violent tremors" of the body as well as shaking and drumming of the palps during various stages of courtship, although there was no mention of audible sounds (Coleman in McKeown 1952). A large wandering spider whose humming sound is regarded as a sign of good luck when heard in African huts may turn out to be another

sparrassid, but perhaps is the widely distributed *H. venatoria* itself (Brady, personal communication).

Vibration in Other Wandering Spiders.—The finding of sound production in a spider that does not use stridulation or percussion to generate its primary signal raises the possibility that some portion of the total sound output of spiders that do use such methods also may be produced by the coincident vibrations of the abdomen or appendages. Such sounds normally would be masked by the louder output of the stridulatory organ or the percussive action. Evidence for this being so was obtained in male *Lycosa rabida* whose palps were fixed to the cephalothorax to prevent palpal stridulation and percussion. A faint whirring sound was detectible when such males were monitored by a vibration pickup, even after the abdomen was attached to the cephalothorax to prevent abdominal oscillations (Rovner 1975). In other words, when one shuts off the primary sound generator, lower-amplitude sounds resulting from appendage oscillations are detectible.

Vibration in Web-weaving Spiders.—In closing, I should like to speculate about the rapid, high-amplitude oscillations seen in certain web-weavers such as araneids when they are disturbed. This behavior ("web flexing") results in the spider becoming blurred; thus, it is hypothesized that the function is to reduce the visual target available to predators or to make onset of contact difficult (Tolbert 1975). In light of the data obtained in the present study, is it possible that such oscillations also mimic the wing-beat frequencies of certain hymenopterans as a means of driving away hymenopteran or other predators? The presence of silk stabilimenta placed radially with respect to the spider would improve the wing-beat mimicry produced by the oscillations, offering yet another hypothesized function for these web structures. To be effective, such a mechanism need not generate sounds audible to our ears but merely displacement waves detectible by arthropods at close range. In other words, is the spider scaring the predator as well as being elusive?

ACKNOWLEDGMENTS

Thanks are due to Willard H. Whitcomb for recommending the collecting area, to Jorge Peña for indicating the specific collecting site, to John J. Kozacik for assistance in preparation of the oscillograms, and to Solveig Sperati Korte for assistance in preparation of sonograms.

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Manuscript received August 1979, revised September 1979.