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Author(s): Walter R. Tschinkel and John T. Doyen

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SOUND PRODUCTION BY SUBSTRATAL TAPPING IN
BEETLES OF THE GENUS *EUSATTUS*
(TENTYRIIDAE: CONIONTINI)

WALTER R. TSCHINKEL AND JOHN T. DOYEN

Department of Biological Science, Florida State University
Tallahassee, FL 32306 and Department of Entomology,
University of California, Berkeley, CA 94720

ABSTRACT

All 3 investigated species of *Eusattus* produce sounds by tapping the substrate with the venter of the abdomen. Tapping by *E. reticulatus* Say and *E. muricatus* LeC. was mostly restricted to the daytime, but *E. robustus* LeC. tapped mostly by night. At 25°C the tap rate of the first 2 species was about 23 to 25 taps/sec, whereas that for the last was about 12 taps/sec. The duration of tapping bursts was radically different for the 3 species, and loudness and details of pattern varied also. The tap-rate of *E. reticulatus* increased linearly with temperature between 25 and 30°C. Behavioral observations showed that only males tapped, and that the level of tapping was increased significantly by the introduction of a female, but not a male, into a male's container. It is hypothesized that the tapping behavior plays some communicatory role in reproductive behavior.

INTRODUCTION

One of the many ways in which insects produce sound for the purpose of communicating is by tapping upon the substrate with part of the body. Such impact-generated sounds have been reported for the ants, *Campanotus ligniperda* and *C. herculeanus* (Markl and Fuchs 1972), termites (Howse 1964), and stoneflies (Rupprecht 1968, 1969), and have been shown in each case to function in communication. Certain woodboring Coleoptera also produce impact sounds (Cymorek 1969), but this mode of sound production seems to be relatively rare among the Coleoptera in general. We report here the discovery that several species of the tentyriid genus *Eusattus* produce stereotyped, species-specific sounds by tapping upon the substrate with the abdominal venter.

MATERIALS AND METHODS

Specimens were collected live at the following localities: *E. reticulatus* from Balmorhea State Park, Toyavale, Reeves County, Texas; *E. muricatus* from Sand Mountain, 18 mi. W. Frenchman, Churchill County, Nevada; and *E. robustus* from West Cove, San Clemente Island, Los Angeles County, California. The beetles were maintained in boxes on sandy substrate with litter and fed bran and rolled oats. Recordings were made using a Uher 4400 Report Portable Tape Recorder, and the recordings were analysed on a Kay Sound Spectrograph. Ambient temperature was noted during recording, but was not varied experimentally. A Rustrak 8-channel Event Recorder was used to record occurrence of tapping by individuals in groups.

RESULTS

All 3 species of *Eusattus* produce sound by tapping the abdominal venter against the substrate, and in all 3 species it is apparently the male which has this behavior. Typically, the beetle raises the entire posterior of the body and brings it forcibly downward so that the point of impact is about the middle of the abdominal venter. The intensity of the sound thus produced depends to a large degree on the substrate, being louder on resonant substrates; but is also obviously a function of the beetle's size, the largest species (*E. robustus*) producing the loudest sounds.

Sound characteristics. Table 1 shows the characteristics of the sounds produced by 3 species of *Eusattus* at about 25°C. In all cases, the sounds consist of a series or burst of rapidly executed taps with a more or less constant rhythm within the burst. Depending upon the species, each burst of taps consists of 20 to 70 taps produced with a characteristic tap-rate. The sounds of the species differ from one another in tap-rate, burst length, number of taps per burst, and loudness. In addition, the sonograms indicated that the bursts of *E. reticulatus* and *E. muricatus* tended to begin softly for the first few taps, hold steady for most taps, and fade out gradually for the last few taps. *E. robustus* began and ended abruptly. Other than the gradual beginning and ending in the first 2 species, there appears to be no modulation of the tap intensity or frequency (rate) within a burst. *E. muricatus* misses occasional taps within a burst, but this seems to be accidental and is without a consistent pattern.

TABLE 1. Signal properties of the tapping signals of several *Eusattus* species. All measurements at 24 to 26°C.

	Mean (\pm S.D.)		
<i>Species</i>	<i>Taps/burst</i>	<i>Burst length (sec.)</i>	<i>Tap rate (Taps/sec)</i>
<i>E. reticulatus</i>	36 (\pm 1.2)	1.20 (\pm 0.06)	30 (\pm 0.6)
<i>E. muricatus</i>	47 (\pm 3.7)	2.02 (\pm 0.18)	23.4 (\pm 1.0)
<i>E. robustus</i>	70 (\pm 13.1)	5.84 (\pm 1.1)	12 (\pm 0.5)

Dependence of tap-rate upon temperature. Except for an evaporative cooler, no temperature control devices were available. We therefore merely recorded the ambient room temperature, which ranged between 24 and 32°C, during the recordings. Within this range, the tap-rate within a burst of *E. reticulatus* increased roughly linearly from about 25 taps/sec to about 38 taps/sec (fig. 1). The number of taps per burst showed no relationship to the temperature. The tap rate of the other 2 species also obviously increased with temperature, but this dependence was not specifically determined.

Possible function of the signals. The most reasonable hypothesis concerning function of this tapping behavior is that it has some kind of signal value, most likely in reproduction. A certain amount of circumstantial evidence supports this notion, for only males have ever been observed tapping. We carried out a few simple experiments on *E. reticulatus* to determine whether or not this behavior might play a role in reproduction.

In the first set of experiments (fig. 2) we tested whether the presence of females or other males had any stimulatory or inhibitory effect upon the tapping behavior. Males were isolated in small plastic boxes with a little

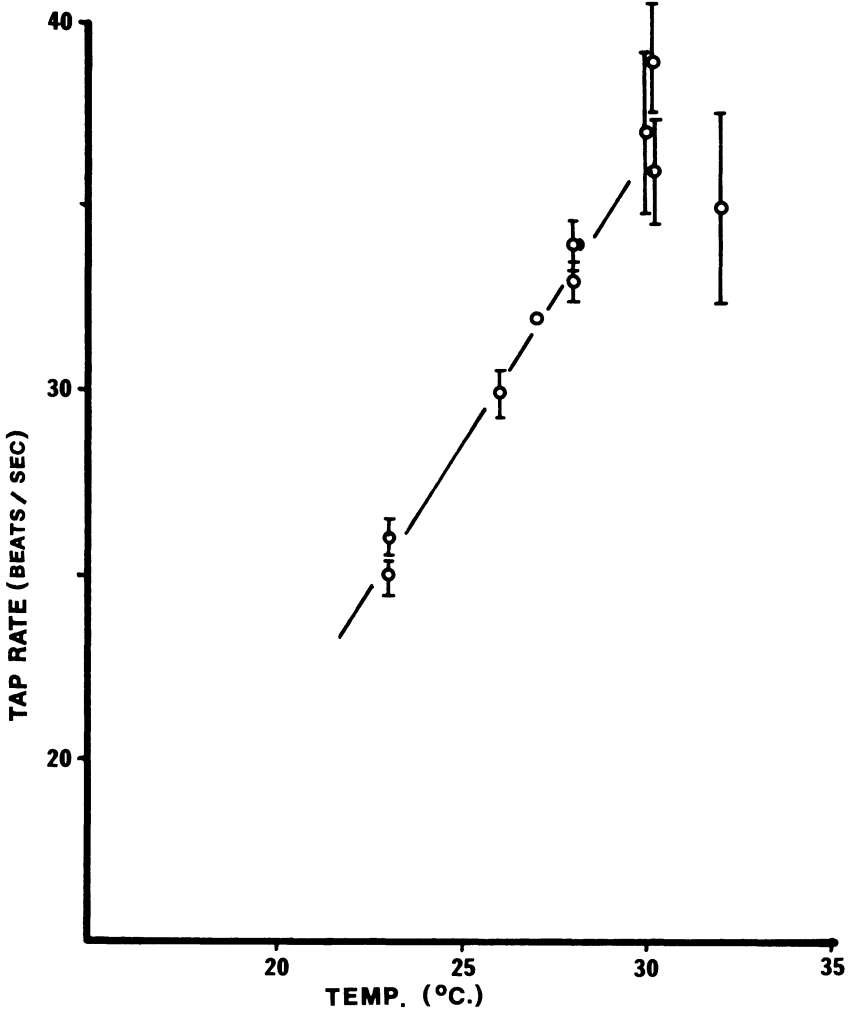


Fig. 1. The tap-rate of *E. reticulatus* as a function of temperature. Each point represents the mean of one individual. The bars are standard deviations.

food. After an acclimation period of several hours, the frequency of bursts of tapping was recorded on an event recorder for $\frac{1}{2}$ hour. Thereupon, a female *E. reticulatus* was placed in the box with the male and the male's tapping was again recorded for $\frac{1}{2}$ hour. The female was then removed and replaced with another male (one of the other males in the same experiment) and the tapping of the resident male recorded. The alien male was then removed and the original male given about 4 hours before its tapping was again recorded while the male was alone. The same procedure was then followed except that the male was introduced first and the female second. The results for 3 such experiments (fig. 1) show that the tapping activity (bursts/ $\frac{1}{2}$ hour) of males is increased significantly ($p < 0.1$) by the introduction of a female, but not by the introduction of a male. In cases where the initial female was replaced with a male, the tapping did not decrease significantly, but this is probably due to a long fade-out period of stimulation by the female rather than to any stimulatory effect by the male. This is supported by experiments in which the male is introduced first.

In isolation over long periods of time, there always occurs some endogenous tapping in the absence of apparent stimulation, and this tapping occurred in bouts rather than being evenly distributed in time. There was a great variation in tendency to tap among the 20 or so *E. reticulatus* males we investigated, ranging from practically zero to very frequently. Some individuals exhibited tapping bouts that lasted several hours, with several bursts per minute.

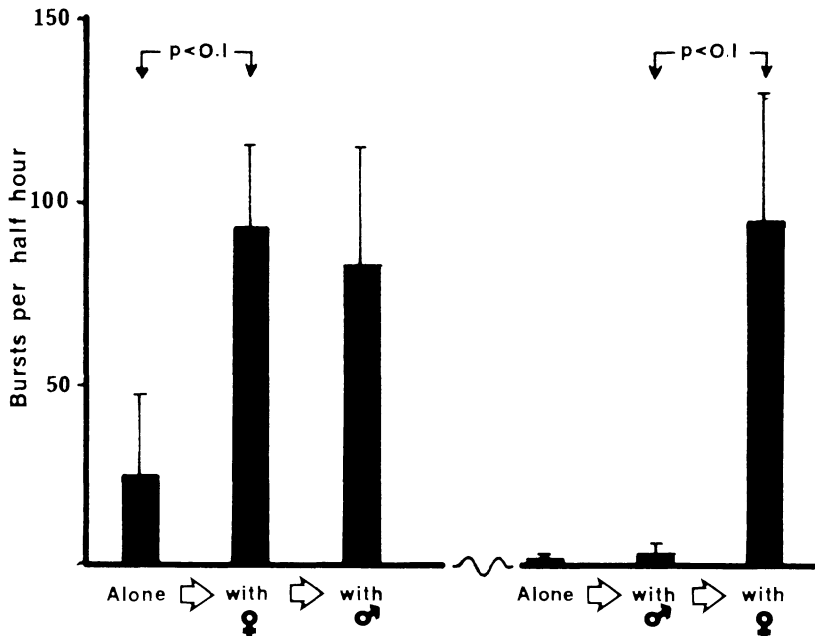


Fig. 2. The effect on burst-frequency of adding either a female or a male to a solitary male *E. reticulatus*. Means of 3 individual test males \pm standard error. Treatment carried out in indicated order, from left to right.

We also tested the possibility that females oriented to and were attracted to tapping males as they are in the South African tentyriid, *Molurodes hirtipes* (V. C. Moran, per. comm.). However, females of *E. reticulatus* showed no significant orientation or attraction to tapping males. It is possible, of course, that conditions were not appropriate for attraction or that females were not receptive, and an attracting function is not ruled out.

DISCUSSION

The possibility of a sexual communicative function of the tapping signal of the flightless, ground dwelling *Eusattus* is indicated by such a function having been demonstrated for a related tentyriid species, *Molurodes hirtipes* (V. C. Moran, pers. comm.). In this South African species, both sexes tap with a sex and species-specific pattern, isolating them reproductively from the sympatric *M. pinguis*. Reproductive isolation could not be a function of the tapping behavior of the *Eusattus* species reported on here, for they are mostly allopatric and are certainly ecologically separated.

In *Molurodes hirtipes*, only the male orients to and is attracted by the female's signal. The female remains stationary upon perceiving the male's signal and responds to his signal with her own. Males also answer other males but are not attracted to them. The sound is substrate borne. Such tapping behavior is very widespread among members of the African tribe Molurini and has been observed in a number of species (unpublished observations). Recently, we have discovered that *Eusattus erosus* and *E. difficilis* as well as several American species of the genus *Coniontis* (tribe Contintini) produce tapping signals. It seems possible that this behavior is widespread among American tentyriids of certain tribes. Even if the purpose of the behavior is not known, it may provide useful information relating to systematic problems.

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