# Seismic signal transmission between burrows of the Cape mole-rat, *Georychus capensis*

Peter M. Narins[1]*, O.J. Reichman[2], Jennifer U.M. Jarvis[3], and Edwin R. Lewis[4]

[1] Department of Biology, University of California, Los Angeles, CA 90024 USA
[2] Division of Biology, Kansas State University, Manhattan, KS 66506 USA
[3] Zoology Department, University of Cape Town, Rondebosch, 7700, South Africa
[4] Department of Electrical Engineering and Computer Sciences, University of California, Berkeley, CA 94720 USA

**Summary.** Both seismic and auditory signals were tested for their propagation characteristics in a field study of the Cape mole-rat *(Georychus capensis)*, a subterranean rodent in the family Bathyergidae. This solitary animal is entirely fossorial and apparently communicates with its conspecifics by alternately drumming its hind legs on the burrow floor. Signal production in this species is sexually dimorphic, and mate attraction is likely mediated primarily by seismic signalling between individuals in neighboring burrows. Measurements within, and at various distances away from, natural burrows suggest that seismic signals propagate at least an order of magnitude better than auditory signals. Moreover, using a mechanical thumper which could be triggered from a tape recording of the mole-rat's seismic signals, we established that the vertically-polarized surface wave (Rayleigh wave) propagates with less attenuation than either of the two horizontally-polarized waves. Thus, we tentatively hypothesize that Rayleigh waves subserve intraspecific communication in this species.

**Key words:** Seismic signals – Mole-rat – Communication – Footdrumming – *Georychus*

## Introduction

Several lower vertebrate species are sensitive to low-level substrate vibrations (Hartline 1971; Ross and Smith 1978; Koyama et al. 1982; Narins and Lewis 1984; Christensen-Dalsgaard and Jørgensen 1988) and some incorporate seismic communication into their behavioral repertoire (Lewis and Narins 1985; Narins 1990). Although note has been made of subterranean rodents producing low-frequency sounds by foot- and head-drumming (e.g. Heteromyidae {Kenagy 1976; Randall

1989}, very little is known of the details of these behaviors. The most convincing evidence for intraspecific communication using seismic signalling in a mammal comes from experimental work with an additional two families of fossorial rodents, Spalacidae and Bathyergidae. The blind mole-rats (Spalacidae) comprise a single genus *(Spalax)* and are restricted to the eastern Mediterranean, eastern Europe, Asia Minor and southern Russia. Spalacid mole-rats provide much of what little is known of seismic and auditory biology in subterranean rodents. Communication behavior is less well-known in the bathyergids, or African mole-rats, of which there are approximately 12 species in 5 genera (Honeycutt et al. 1987). Bathyergidae occur in sub-Saharan Africa and are colloquially known as blesmols or mole-rats (Smithers 1983).

The subjects of this paper, *Georychus capensis,* the Cape mole-rat, occur in underground burrows in sandy clay soils, and are autochthonous to the Cape region of South Africa (Smithers 1983). This monotypic genus appears to be most closely related to two other solitary mole-rat genera, *Heliophobius* and *Bathyergus,* and less closely related to social *Cryptomys* and *Heterocephalus* within the Bathyergidae (Honeycutt et al. 1991). *Georychus, Cryptomys* and *Bathyergus* occur sympatrically in some areas of the Cape Province (Walker 1975; Reichman and Jarvis 1989). *Georychus* have mean head and body lengths of 18.4 cm (15.3–20.0) in males, 17.7 cm (14.3–20.4) for females (Smithers 1983) and mean body weight of 181 g (Bennett and Jarvis 1988a) with a maximum of 360 g (Smithers 1983).

*Georychus* construct complex burrow systems of approximately 130 m length and mean diameter 10 cm. These incorporate nest cavities, food storage tunnels (DuToit et al. 1985), and possibly, as in *Bathyergus* and *Cryptomys* burrows, blind-ended defecation chambers (Davies and Jarvis 1986). Openings to the burrow systems are quickly plugged with soil. Because each burrow is essentially a closed and sealed system, its humidity may be higher and its $CO_2$ and temperature more constant than that at the surface, as has been found within the

closed, similarly complex burrows of other fossorial forms of mammals (Altuna 1983, 1985; Reichman and Smith 1990). Cape mole-rats extend superficial burrow tunnels to obtain their foods, primarily the roots and underground storage organs of plants, although 6.9% of their diet consists of green above-root (aereal) plant materials which are occasionally pulled down into the burrow with the roots (DuToit et al. 1985).

*Georychus* burrow systems approach within one meter of each other and appear to be evenly spaced (Davies and Jarvis 1986; Bennett and Jarvis 1988a), as has been noted for other fossorial rodents (Reichman et al. 1982). *Georychus* produces footdrums in the laboratory and in the field, and it is possible that these signals are used for maintenance of spacing patterns and communication between individuals. Emanating from within their burrows, the footdrumming signals contain both auditory and seismic components. However, in tests with spalacid mole-rats *(Spalax)*, reseachers have segregated air-borne auditory and soil-borne seismic components of the signal. In laboratory studies, Rado et al. (1987) have determined that *Spalax* detect their signals seismically rather than through the airspace of burrows.

Using recordings obtained from microphones and geophones, and playback experiments conducted with a mechanical thumper, we were able to characterize the communication modes of *Georychus* and secure preliminary evidence as to their function. We conducted our investigation of the communication systems of *Georychus* both in the laboratory and in the animal's natural habitat in order to (1) document the temporal characteristics of the animal's seismic signals; (2) measure the auditory and seismic transmission properties of the local substrate and to document the effect of this substrate on both the horizontal and vertical components of the signals when propagating between natural burrow systems; and (3) record the animal's response to substrate vibrations introduced in the burrow.

## Materials and methods

*Footdrumming recording.* In the laboratory, a male and a female mole-rat were placed in cylindrical plexiglass tubes (length: 0.8 m) connected to a central common chamber; the animals were physically separated by a hardboard partition in the center of the chamber. The distal ends of the plexiglass cylinders were each fitted with a plastic box which served as a refuge for the animals. Thus, auditory and seismic signals generated by one animal could be detected by the other. We measured the airborne signals produced by footdrumming of the female using a small lapel microphone (Realistic; 50–15000 Hz) taped to the plastic refuge chamber in which the female was located. The male's thumps were registered with a directional microphone (AKG CE–8; ±2 dB, 100–20000 Hz) mounted on a mini-tripod and placed within 0.5 cm of the plexiglass cylinder in which he was stationed. During lab recordings the animals were separated by a distance of 1 m. We refer to each strike of the mole-rat's foot as a footdrum; a discrete sequence of footdrums as a footroll, and an individually distinct series of footrolls as a footroll sequence, following the nomenclature of Randall (1984, 1989).

*Synthetic seismic signal production.* In the field, males and females of the mole-rat *Georychus capensis* are solitary in that they are each

exclusive occupants of one tunnel system (DuToit et al. 1985). In a community of mole-rats located in an open field near the campus of the University of Cape Town (33°59′S and 18°36′E), we captured and removed the mole-rats in two adjacent burrow systems which we designated A and B. By systematically probing into successive tunnel sections with a sharp stick, we were able to map out the main tunnels and several side tunnels in each burrow system. We then repaired the probe-holes and a mechanical thump generator was inserted at the end of a side tunnel in burrow system A. The location of the thump generator was invariant throughout the experiments. In addition, 3 simulated burrows were excavated at distances of 1.0, 1.7 and 2.3 m from the thumper position in burrow system A. From each burrow (approximately 30 cm long) both seismic and auditory measurements could be made. At the end of the study, the empty burrow systems were excavated and burrow depth and diameter were measured.

Seismic stimuli were produced with a mechanical thumper constructed from the solenoid of an impact printer (Moore et al. 1989). The thumper was configured such that the printer solenoid was mounted at the end of a piece of weighted aluminum channel bracket (36 cm × 4.3 cm) and was adjusted so that the piston struck a hard rubber circular pad (diameter 15 mm) mounted at the end of the bracket. The channel bracket could then be conveniently inserted 50 cm into a *Georychus* burrow, while ensuring that the rubber pad was in solid contact with the substrate. The solenoid was driven by a pulse or series of pulses from a driver located on the channel bracket. The driver in turn was activated by a trigger circuit (Moore et al. 1989) which generated standard pulses of constant duration (0.45 ms) and level ($-0.8$ V to $+6.3$ V) suitable for the driver circuit. The trigger circuit received its input from a stereo tape player (Sony WM–D6) containing an endless cassette on which was prerecorded either (1) a series of 2.5 ms negative-going pulses with a repetition period of 900 ms, or (2) a recording of courtship thumping by a female *Georychus*.

*Auditory and seismic signal measurements and analysis.* A directional microphone (AKG CE8) and preamplifier (AKG SE5E–10) were placed in a specially-constructed protective wire housing and inserted into an occupied *Georychus* burrow system for monitoring airborne sounds. The wire housing provided necessary protection against damage by mole-rats, and caused negligible distortion at the frequencies of interest ( < 4 kHz). Auditory signals were recorded on a two-channel tape recorder (Stellavox SP8; 30–20000 Hz) at 19 cm/s for subsequent analysis. Sound intensities in the burrow were measured using a calibrated precision sound level meter equipped with an octave-band filter (GenRad 1982). For all readings, the fast detector (time constant: 125 ms) of the sound level meter was used and the analog meter was carefully monitored for the presence of any visible needle movement during the thump playback experiment.

Substrate vibrations were measured with an array of 3 geophones (AMF Industries 10395; peak response: 10 Hz; sensitivity: $1.0 × 10^4$ mV/m/s) orthogonally mounted on an aluminum plate (9.6 cm × 12.0 cm) fitted with 3 legs (7.3 cm) for securing the plate to the soil. This arrangement allowed independent recording of the seismic signal in 3 planes. It was important to achieve a solid mechanical coupling of the geophone array to the substrate, to minimize measurement error of the local substrate particle velocity. Each geophone output was separately amplified with a battery-powered, variable gain preamplifier and recorded on a separate channel of a 4-track portable FM cassette data recorder (Teac R–61). The fourth channel of the cassette data recorder was used either in the direct mode (freq. resp.: 50–8000 Hz) for making measurements of the sound of the thumper or of the animal, or in the FM mode for recording the trigger signal from the pre-recorded endless cassette. The geophone array was placed at known distances from the thumper location, either on a line in the substrate leading away from a burrow, or directly over a burrow itself.

Auditory and seismic signals were analyzed using either a real-time DSP Sonagraph (Kay 5500) or a calibrated, averaging dynamic signal analyzer (Hewlett-Packard 3561A). The latter instrument

could be triggered by the periodic (900 ms) pulses from channel four of the cassette data recorder. All geophone responses evoked by the periodic thumps were averaged 32 or 50 times and plotted.

Each geophone was individually calibrated in the laboratory by subjecting them to a known acceleration produced by a vibration exciter (Brüel & Kjaer 4809) driven by a controller (Brüel & Kjaer 1047). Using a constant acceleration (measured with a calibrated accelerometer [Brüel & Kjaer 8306]) of 0.2 m/s$^2$, the sensitivity of each geophone was determined over the frequency range from 4–500 Hz.

*Behavioral measurements of* Georychus. Two female *Georychus* were live-trapped by one of us (JUMJ), fitted with a radio collar and tilt switch (BioTrack SR1) and released back into their own burrow systems. The movements of the animals in response to synthetic courtship thumps caused the tilt switch to activate, changing the transmitter output rate between 45 and 125 ppm. The transmitter signal was monitored with a portable receiver (Mariner Radar M57) fitted with either a loop or 3-element Yagi antenna. The auditory output of the receiver was detected by a small lapel microphone (Realistic) and recorded on one channel of the 4-channel cassette tape recorder (Teach R61); the geophone outputs were recorded on the remaining 3 channels. The animals' movements were monitored continuously for 60 s as a baseline control. This was followed by 21 trials consisting of 10 s of artificial (male) thump playback with the thumper placed within 0.5 m of the burrow, and 60 s of movement monitoring. Post-stimulatory movements were scored in 10-s intervals as an unambiguous pulse rate shift; i.e., the presence of at least two pulses at the increased (or decreased) pulse rate.

## Results

### Measurements of captive animals

The auditory waveforms generated in the laboratory by a typical foot-thumping interaction between the male and female mole-rats are displayed in Fig. 1. The strict 1:1 following response between male and female was observed in virtually every interaction recorded. During the portion of the interaction illustrated, the female led the male for the majority of the thumps. This pattern was not invariant, however; extensive analyses of thumping interactions between pairs of captive mole-rats revealed that the lead often switched between the two participants in a duet, although no consistent leader-follower pattern or lead-switching periodicity could be discerned. In the laboratory the mole-rats would be very likely able to detect each others' auditory as well as seismic signals. Thus the entrainment observed between pairs of captive *Georychus* could likely be mediated by either or both of the aforementioned cues.

### Field measurements

*Burrow geometry.* The tunnel cross-sectional diameter and depth were measured at each recording site in two adjacent burrow systems (4 sites in burrow system A and 5 sites in burrow system B). We found that in one of the vacant tunnels that we studied (burrow system A), the mean tunnel cross-sectional diameter varied little over a distance of 3.0 m (62.5 ± 8.7 mm SD), but that the mean distance from the tunnel bottom to the surface was more variable (127.5 ± 69.0 mm SD). The other abandoned
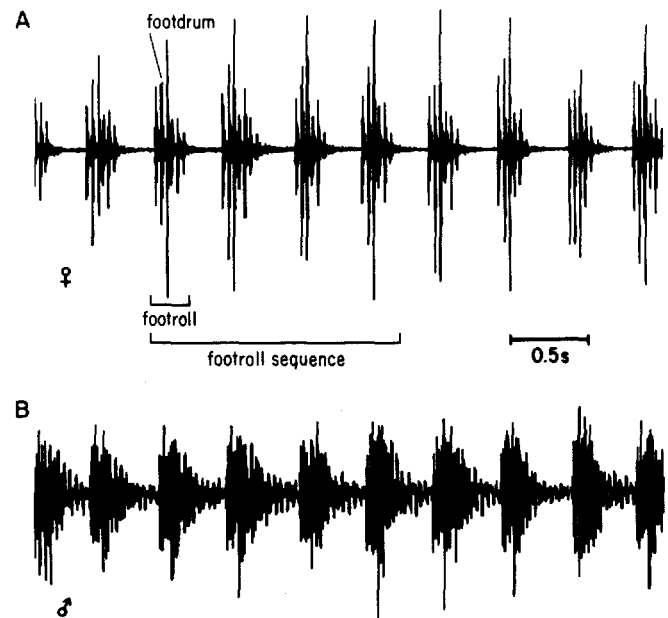


**Fig. 1.** Simultaneously-recorded auditory waveforms of the thumps produced during a footroll sequence by a female (**A**) and a male (**B**) mole-rat. The animals were separated by a transparent divider located in a plexiglass tunnel system through which they could travel. Note the 1:1 synchrony of the footrolls throughout this interaction. Temperature during recording: 24.5 °C

burrow system (B) was located 3.4 m from system A at its closest approach. Burrow system B had a mean tunnel cross-sectional diameter measured over a 2.3 m distance of 54.5 ± 5.7 mm SD, and the mean distance from the tunnel bottom to the surface was 106.0 ± 11.4 mm SD.

*Propagation characteristics of seismic signals.* To quantify the degree to which the seismic signals propagate in the substrate, we measured the attenuation of an artificial mole-rat thump at a series of distances from the mechanical thumper. For each measurement, the geophone array was moved and the thumper remained fixed at the same location in burrow system A. Because the trigger for the thumper in this experiment was derived from a tape of a female mole-rat drumming in the lab, the trigger signal was aperiodic since each footroll contained a variable number of footdrums; thus the responses were not amenable to signal averaging. The responses of the 3 orthogonal geophones at progressively increasing distances from the thumper are shown in Fig. 2. From the responses to a single footroll sequence from the thumper, it is clear that the vertically-oriented geophone-receives the seismic component with the greatest velocity amplitude for distances up to 3 m, but that this component also suffers more attenuation than the others and is reduced below the others at distances greater than ca. 4 m.

In order to improve the signal-to-noise ratio of the seismic signals recorded from distances greater than 4 m, it was necessary to drive the thumper with a periodic trigger signal, thus facilitating signal averaging (see Methods). The periodic thumper waveforms produced
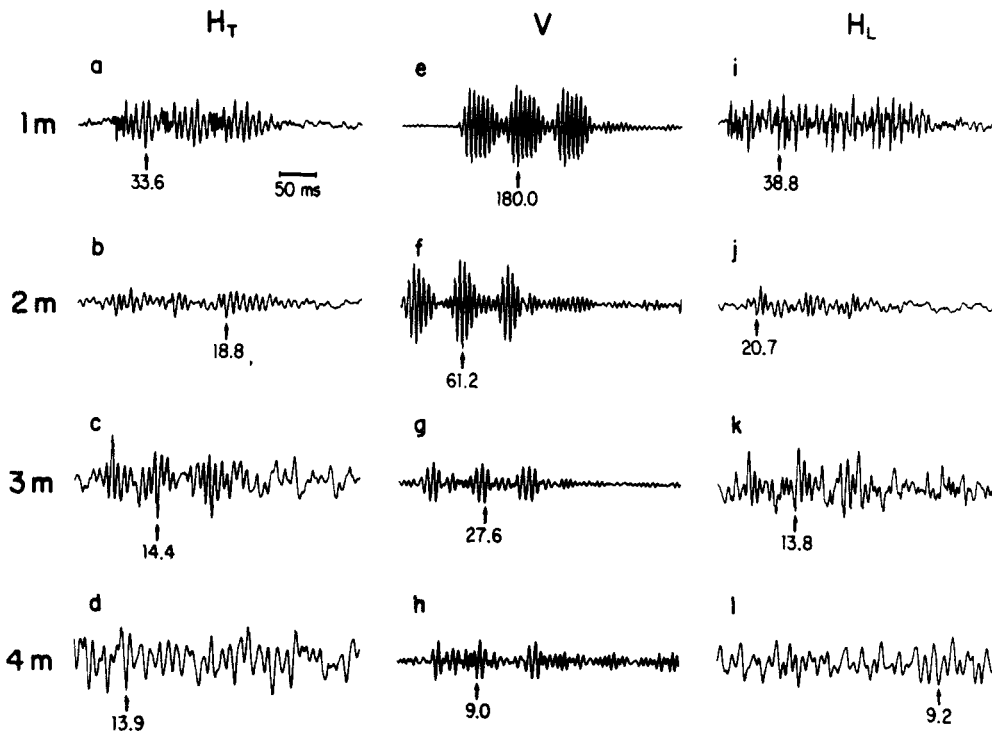
**Fig. 2.** Electrical waveforms representing simulated footdrumming of a mole-rat as received by a set of geophones placed at various distances from the thump generator. Geophones were oriented horizontally and transverse to the axis of propagation ($H_T$), horizontally and longitudinal to the axis of propagation ($H_L$), and vertically (V). Values shown are the maximum peak-to-peak substrate particle velocities indicated by arrows, and are coefficients of $1 \times 10^{-6}$ m/s
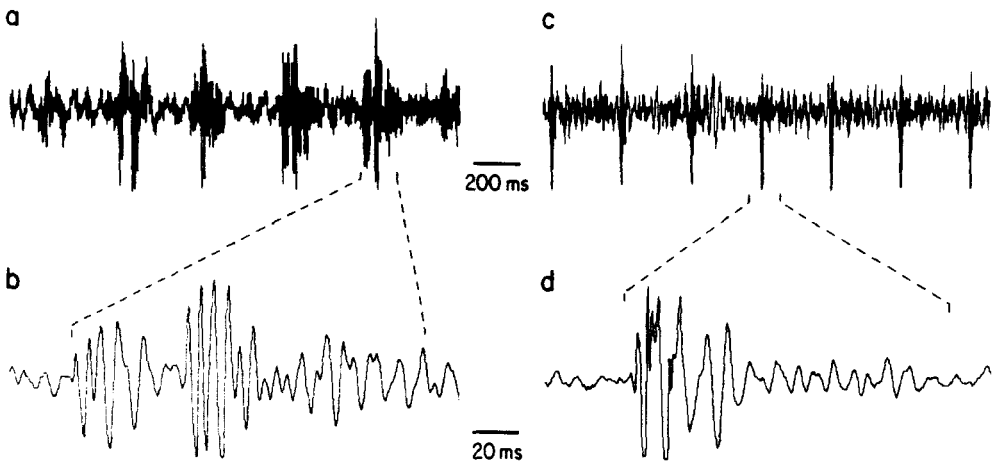


**Fig. 3. a** Auditory waveform showing a footroll sequence produced by a male mole-rat, *Georychus capensis*. **b** A single footroll from (**a**) is displayed with an expanded time scale. Similarly, a series of simulated male thumps is shown in (**c**) and a single simulated thump is shown expanded in (**d**)

by a train of trigger pulses closely resemble those generated by the mole-rat (Fig. 3). The maximum peak-to-peak substrate particle velocities registered by each of the 3 geophones for one set of measurements are reported as a function of distance from the thumper in Table 1. From the data in this Table, it is apparent that the attenuation rate of the vertical velocity component of the thump is more than twice as great as that for either of its two horizontal components. As a result, for distances less than 4.0 m from the source in this example, the vertical substrate velocity component is larger than either of the two horizontal components. However, for distances greater than 4.0 m, the horizontal velocity components become greater than the vertical component.

*Inter-burrow signal transmission.* We next measured the ability of the periodic seismic signal from the thumper to propagate between two natural, abandoned mole-rat

**Table 1.** Values representing the maximum peak-to-peak substrate particle velocity obtained by averaging the responses to 50 simulated mole-rat thumps. Three geophones were positioned at various distances from the thumper, and were oriented orthogonally as follows: horizontally and transverse to the axis of propagation ($H_T$), horizontally and longitudinal to the axis of propagation ($H_L$), and vertically (V)

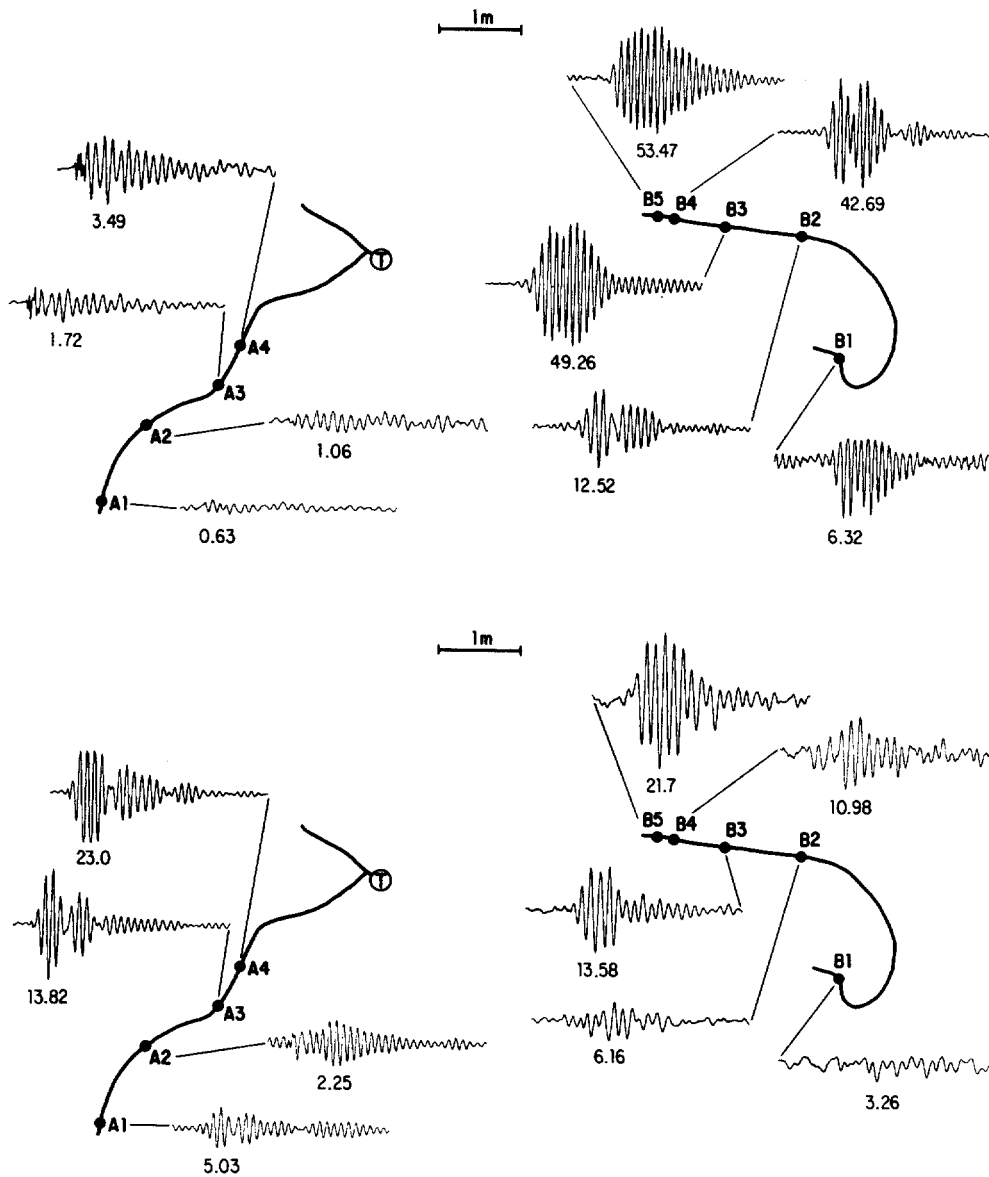| Distance (m) | Velocity (m/s × 10⁻⁶) | | |
|---|---|---|---|
| | $H_T$ | V | $H_L$ |
| 1.0 | 28.5 | 163.6 | 27.0 |
| 2.0 | 11.4 | 62.0 | 13.3 |
| 2.5 | 14.7 | 33.8 | 8.8 |
| 3.0 | 16.0 | 30.2 | 12.4 |
| 3.5 | 7.2 | 15.2 | 5.9 |
| 4.0 | 8.6 | 8.4 | 9.2 |
| 5.0 | 5.6 | 4.6 | 7.3 |
| 7.0 | 2.8 | 2.1 | 2.7 |
| 8.0 | 2.6 | 1.4 | 2.9 |

**Fig. 4.** Scale drawing of portions of two natural, vacant burrow systems of the Cape mole-rat. Magnitude of the vertical component of simulated thumps generated by the thumper at T measured by geophones placed at various locations above 2 mole-rat burrow systems, A and B. Each waveform represents the average velocity of 32 thumps. The value shown is the maximum peak-to-peak particle velocity of these averages and is a coefficient of $1 \times 10^{-6}$ m/s. (Note: not all waveforms have the same vertical scale.) Straight-line distances from the thumper to the recording sites are A1: 4.5 m; A2: 3.5 m; A3: 2.5 m; A4: 2.0 m; B1: 5.7 m; B2: 5.1 m; B3: 4.2 m; B4: 3.6 m; B5: 3.4 m



**Fig. 5.** Magnitude of the horizontal longitudinal ($H_L$) component of simulated thumps generated by the thumper at T as measured by geophones placed at various locations above 2 mole-rat burrow systems, A and B. Other parameters same as Fig. 4

burrows. The geophone array was placed at increasing distances from the thumper over burrow system A, as well as over burrow system B. Figures 4 and 5 illustrate the vertical and horizontal longitudinal components of the seismic waveforms and the peak-to-peak amplitudes of the mean ($n=32$) particle velocities recorded from several points over each of the two burrow systems. Both signal components appear to attenuate more rapidly within the source burrow (A) than between burrows. To quantify this, the particle velocity as a function of distance for two seismic components recorded from both burrow systems has been plotted in Fig. 6. The attenuation rate of the vertical seismic component measured at burrow B is $-21 \times 10^{-6}$ m/s/m, whereas that for the horizontal seismic component is $-5.9 \times 10^{-6}$ m/s/m. In contrast, the attenuation rate of the vertical seismic component measured in burrow A is $-1.1 \times 10^{-6}$ m/s/m, whereas that for the horizontal seismic component in burrow A is $-6.5 \times 10^{-6}$ m/s/m.
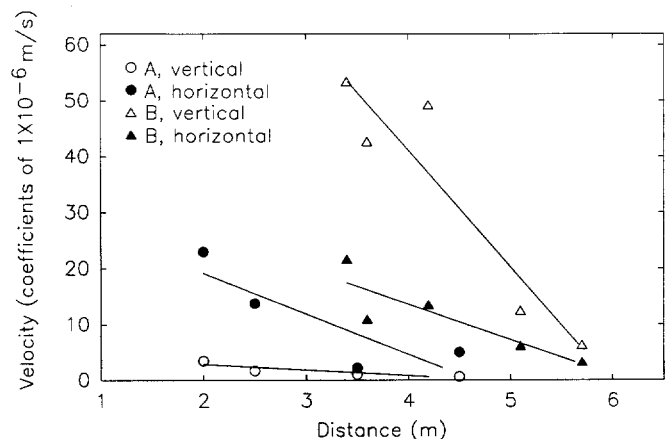


**Fig. 6.** Average ($n=32$) maximum substrate particle velocity of artificial thumps, measured with geophones, plotted against the distance from the thump generator located in burrow system A. Vertical and horizontal longitudinal geophones were placed in the ground above burrow systems A and B
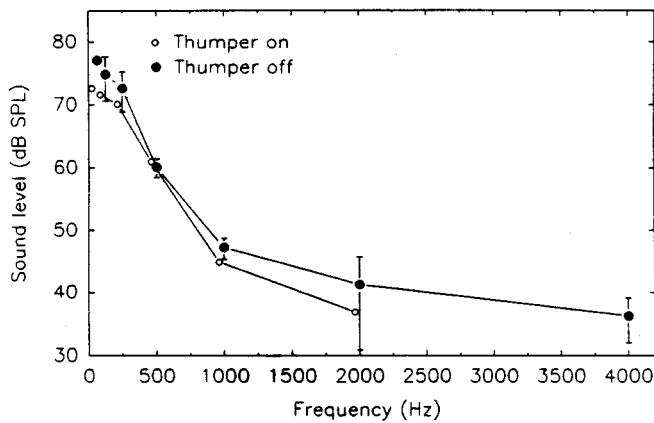
**Fig. 7.** Octave-band sound levels measured within a freshly dug (simulated) burrow located 1 m from the thump generator plotted as a function of octave band center frequency. *Filled circles:* mean of 5 background noise measurements for which the standard deviations are also plotted. *Open circles* (shifted to the left by 30 Hz for clarity): a single measurement during thumper activity

The average ($n = 32$) latency, or propagation time between the initiation of a thump in burrow A and its arrival at different points above both burrow system B as well as above a simulated burrow (SB) excavated between the two natural burrows, was also measured. These latencies were plotted against the distance separating the thump generator and the geophones. The best-fit regression lines through the data have slopes of 12.29 ms/m and 8.75 ms/m for the simulated burrow and burrow system B, respectively. From these values, propagation velocities of 81.4 m/s and 114.3 m/s were calculated. The mean of these two propagation velocities is 97.9 m/s.

To determine whether a seismic signal from a mole-rat would produce audible sound in a neighboring burrow, we set up the thumper in burrow system A and placed the sound level meter in the simulated burrow 1 m from the seismic source. The octave-band sound levels measured in the simulated burrow before and during thumper activation are shown in Fig. 7. During none of these measurements could any visible movement of the analog meter needle be detected. Note that the auditory component of the thumper is indistinguishable from the background noise under these conditions.

*Response of females to artificial thumps.* This experiment was carried out to determine if artificially-produced mole rat thumps would induce movement and/or footdrumming by a resident female. Figure 8 shows the result of a typical trial in which the thumper was placed in the vicinity of a burrow occupied by a female *Georychus*. In 17 out of 21 trials, the simulated male footdrumming delivered by the mechanical thumper was followed by movement of the female in her burrow; moreover, the highest probability of movement occurred between 10 and 20 s post-stimulus and declined continuously throughout the monitoring interval until the next stimulus. Neither random hand- or foot-tapping by the experimenters nor passing truck traffic nearby resulted in
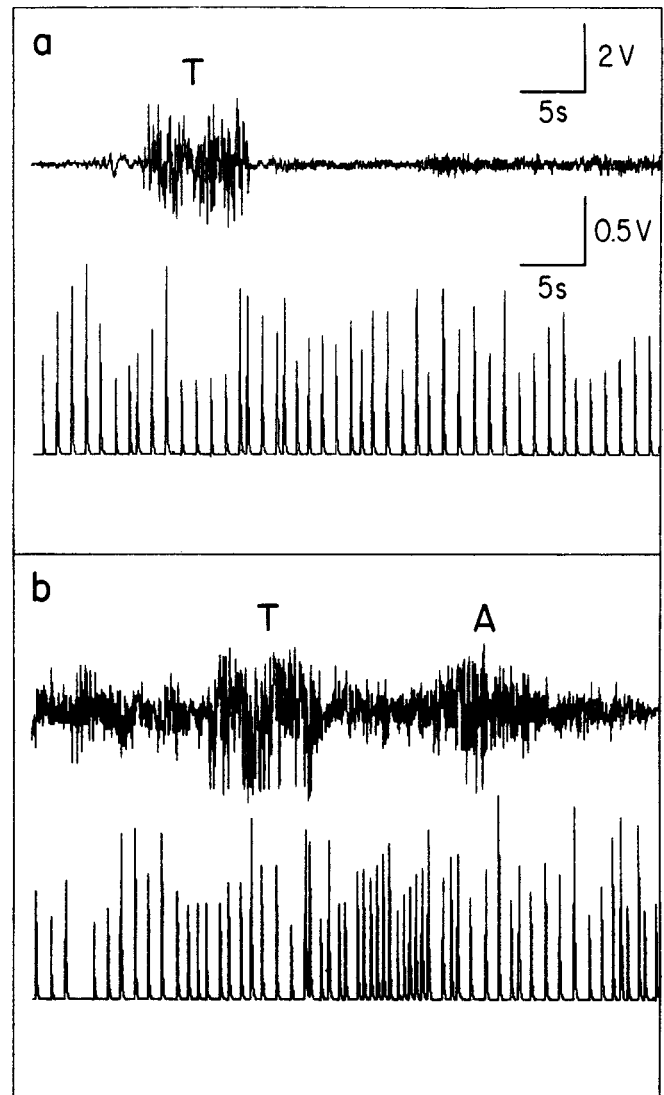


**Fig. 8.** Top traces in (**a**) and (**b**) show an auditory waveform of the courtship thump, *T*, produced by a male mole-rat and played back using an mechanical thumper to a conspecific female in her burrow; bottom traces: output of a movement-sensitive radio collar worn by the female. A pulse rate shift in the emitted radio signal indicates movement by the mole-rat. In (**a**), synthetic thump T evoked no position change in the female. In (**b**), the female changed her position in response to thump T as seen by the change in the rate of signal production. This is followed by a truck passing nearby which produced an artifact, *A*. Calibration bars refer to both panels

either reliable female movement or footdrumming. In none of the 21 trials did the mechanical thumper evoke footdrumming by the test female.

**Discussion**

That footdrumming signals of *Georychus* are detected as seismic communication signals is supported by the combination of (1) measurements of propagated soil-borne vibration between *Georychus* burrows which are signifi-

cantly above the background noise level; (2) vanishingly low levels of propagated air-borne signals which are indistinguishable from background noise measured in an adjacent burrow; (3) saliency of the vertically-polarized component of the vibration after transmission in soil over distances approximately corresponding to that between burrows; (4) complexity of the seismic signals which may relay both presence and sex of the individual; and (5) behavioral data indicating females of *Georychus* detect these seismic signals. Drumming and listening behaviors of *Spalax* (Rado et al. 1987), the predominantly low frequency components (below 1 kHz) of the vibration signals of *Spalax* (Heth et al. 1987), low frequency (less than 2.0 kHz) sound sensitivities of *Spalax* (Bruns et al. 1988), *Cryptomys* (Burda et al. 1988; Mueller and Burda 1989), *Dipodomys* (Rupert and Moushegian 1970), and *Talpa* (Aitkin et al. 1982), and ear architecture in *Spalax* (Burda et al. 1989) and heteromyids (Webster and Webster 1972, 1980) corroborate this evidence for seismic communication.

The importance of drumming signals in communication is emphasized by studies of *Georychus* on the association between drumming, increase in testosterone levels in males, and female response drumming (Bennett and Jarvis 1988a). Related studies of heteromyids (Randall 1989) suggest that between-individual variation in drumming not only signals the presence of but also provides information regarding the identity of the drummer. Among the strictly subterranean *Georychus*, both males and females drum by alternately striking both feet on the floor of the burrow. Males may drum continuously for up to 2 min. Territorial drumming is similar in both sexes; however, during the breeding season the footdrumming rate in males (26/s) and females (15/s) is sexually dimorphic (Bennett and Jarvis 1988a) suggesting once again the role of drumming as a communication signal.

Despite the sexual dimorphism in footdrumming rates, we have shown that during a communicative interaction, individual *footrolls* are most often entrained, thus reflecting a deliberate attempt by both males and females to maintain 1:1 synchronization. The purpose of footroll entrainment in mole-rats is unknown, but various functions have been ascribed to synchrony of communication signals in other systems such as (1) firefly flashing [avoidance of disruption of species-specific rhythm used by females to localize the swarm, and identification of specific mating sites (Lloyd 1973, 1983)], (2) synchronous glowing of ostracods [predator evasion and intraspecific communication (Morin 1986)], and (3) entrainment of frog calls [optimization of information transmission in a chorus (Brush and Narins 1989)].

Seismic propagation experiments in the sandy soil inhabited by *Georychus* reveal that the horizontal and vertical components of substrate particle velocity suffer different attenuation rates. In theory, therefore, mole-rats could obtain a reasonable estimate of the distance to a footdrumming conspecific neighbor from simultaneous comparisons of the relative magnitudes of the horizontal and vertical substrate velocity components. There are presently no data, however, to suggest that such a comparison is possible. We may only speculate at present that such information could be useful in maintaining appropriate spacing between individuals, as occurs with other fossorial rodents (Reichman et al. 1982). It is known that outside the context of reproduction, if two *Georychus* are introduced into the same burrow, aggression and fighting can escalate until one animal is killed (JUM Jarvis, personal observations).

In addition, our propagation experiments demonstrate that mechanically-generated seismic signals designed to mimic the gross structure of naturally-occurring mole-rat footdrums are indeed propagated and are present above the ambient noise level at natural interburrow distances (3–4 m). The vertical substrate velocity component of the propagated wave measured in burrow B, for example, exhibits a relatively large amplitude, but suffers a greater *rate* of attenuation than the horizontal seismic component. The low rate of attenuation of the vertical seismic component measured in burrow A is due to the small absolute amplitude of this component. This, in turn, is likely due to the position of the geophone array (on top of the burrow) relative to the mechanical thumper (in the bottom of the same burrow). Thus the propagation path from the thumper to the geophones over burrow A would of necessity be circuitous resulting in an amplitude loss, an effect which would be minimized for signals traveling between burrows. Perhaps this result would have been different had the geophones been placed in the burrow.

This idea is strengthened by the latency measurements for signals received in both burrows: velocities of propagation (reciprocal of latencies) are longer for burrow A than for burrow B. The mean propagation velocity for the two burrows, however, is 97.9 m/s, which closely corresponds to the published velocity of Rayleigh wave transmission in moist soil of ca. 100 m/s, roughly 1/3 the velocity of sound in air (Lewis and Narins 1985).

Measurements of acoustic propagation between burrows clearly demonstrate the inadequacy of airborne sound as a medium for subterranean, interburrow information transmission. Although the thumper produced both a seismic and an auditory component when it strikes the substrate, the auditory signal measured in the simulated burrow is indistinguishable from the background noise (Fig. 7). Thus, airborne cues appear to be strongly attenuated by the intervening substrate as well as the soil-air interface. Although these results do not preclude the reception of the airborne component of the signal by *Georychus*, they are consistent with the observation that *Spalax* ignores acoustic portions of the thump signal in the laboratory and responds only to its seismic component (Rado et al. 1987).

Playback experiments in which artificial, mechanically-generated thumps are introduced into the soil in close proximity to an inhabited mole-rat burrow revealed that the thumps elicited movement by the female residents in 17 out of 21 trials. Moreover, that movement was most likely to occur from 10–20 s post-stimulus, followed by a declining probability of movement thereafter, indicates a response to the artificial thumps. However, in no case did the mechanical thumper evoke foot-

**Table 2.** Relationship between social system and dominant mode(s) of communication in mole-rats in the family Bathyergidae

| Genus | Social System | Mode of Communication | References |
|---|---|---|---|
| *Heterocephalus* | Eusocial | Tactile, olfactory<br>Some acoustic | Jarvis (1981, 1991)<br>Lacey et al. (1991)<br>Pepper et al. (1991) |
| *Cryptomys* | Social | Tactile, some olfactory<br>acoustic, some seismic | Bennett (1988), Burda (1989)<br>Bennett and Jarvis (1988b)<br>Bennett (1988, 1989) |
| *Bathyergus*<br>*Heliophobius*<br>*Georychus* | Solitary | Seismic, acoustic<br>Unknown<br>Seismic, acoustic | Jarvis and Bennett (1991)<br><br>Bennett and Jarvis (1988a) |

drumming from the female under test. This observation may not be unexpected given the fact that the artificial thumps in our experimental paradigm appear to have arisen de novo in both space and time, without what would surely be a preamble of digging sounds or other indication of a neighbor's presence had they been generated by a conspecific male.

We believe the available evidence supports the hypothesis that seismic signalling occurs between individuals of the Cape mole-rat, *Georychus capensis*. This communication modality appears eminently suited to solitary, subterranean animals which inhabit burrows separated by dense, homogeneous soil[1]. It is also possible that digging sounds are detected by neighbors and could also serve as territorial advertisement in both solitary and social genera. The extensive work on the blind mole-rats (Rado et al. 1987; Heth et al. 1987) and preliminary evidence for North American pocket gophers (Reichman, pers. obs.), in addition to the evidence presented herein, suggest that seismic signalling may be a widespread phenomenon among subterranean organisms.

In addition to seismic communication between burrow inhabitants, those species of bathyergids that are colonial or eusocial (e.g., *Heterocephalus*, *Cryptomys*) appear to incorporate tactile and olfactory communication into their repertoire (Sherman et al. 1991; Table 2). These communication modalities would be ineffective for communication through the dense medium of the soil, but within a burrow they would serve as efficient means for communication among blind individuals. The proposed relationships between the social system and the dominant mode(s) of communication in the 5 genera of mole-rats in the family Bathyergidae are shown in Table 2. It is here suggested that the more solitary the mole-rat, the more it relies on seismic communication to signal to animals in neighboring burrow systems. Future investigations should include surveys of other fossorial forms to determine whether they utilize seismic communication, and playback experiments to confirm and decipher the signals being transmitted and received by the participants.

---

[1] However, once the animals have come together, vocalizations supplement the seismic signalling and dominate when the animals are in close proximity (Bennett and Jarvis 1988a). This seems to be also true for *Bathyergus suillus*, another solitary bathyergid (Jarvis and Bennett 1991)

## References

Aitkin LM, Horseman BG, Bush BMH (1982) Some aspects of the auditory pathway and audition in the European mole, *Talpa europaea*. Brain Behav Evol 21:49–59

Altuna CA (1983) Sobre la estructura de las construcciones de *Ctenomys pearsoni* Lessa y Langguth, 1983 (Rodentia, Octodontidae). Res Com Jorn C Nat Montevideo 3:70–72

Altuna CA (1985) Microclima de cuevas de *Ctenomys pearsoni* (Rodentia, Octodontidae) en Arroyo Carrasco (Montevideo). Actas Jorn Zool Uruguay 1985:59–60

Bennett NC (1988) The trend toward sociality in three species of Southern African mole-rats (Bathyergidae): Causes and consequences. Ph.D. thesis, University of Cape Town

Bennett NC (1989) The social structure and reproductive biology of the common mole-rat, *Cryptomys h. hottentotus* and remarks on the trends and reproduction and sociality in the family Bathyergidae. J Zool (Lond) 219:45–59

Bennett NC, Jarvis JUM (1988a) The reproductive biology of the Cape mole-rat, *Georychus capensis* (Rodentia, Bathyergidae). J Zool (Lond) 214:95–106

Bennett NC, Jarvis JUM (1988b) The social structure and reproductive biology of colonies of the mole-rat, *Cryptomys damearensis* (Rodentia, Bathyergidae). J Mammal 69:293–302

Bruns V, Mueller M, Hofer W, Heth G, Nevo E (1988) Inner ear structure and electrophysiological audiograms of the subterranean mole rat, *Spalax ehrenbergi*. Hearing Res 33:1–10

Brush JS, Narins PM (1989) Chorus dynamics of a neotropical amphibian assemblage: Comparison of computer simulation and natural behaviour. Anim Behav 37:33–44

Burda H (1989) Reproductive biology (Behaviour, breeding and postnatal development) in subterranean mole-rats *Cryptomys hottentotus* (Bathyergidae). Z Säugetierkd 54:360–376

Burda H, Mueller M, Bruns V (1988) The auditory system in subterranean mammals. In: Elsner N, Barth FG (eds) Sense organs – interfaces between environment and behaviour. G. Thieme, Stuttgart, p 182

Burda H, Bruns V, Nevo E (1989) Middle ear and cochlear receptors in the subterranean mole-rat, *Spalax ehrenbergi*. Hearing Res 39:225–230

Christensen-Dalsgaard J, Jørgensen MB (1988) The response characteristics of vibration-sensitive saccular fibers in the grass-frog. J Comp Physiol A 162:633–638

Davies KC, Jarvis JUM (1986) The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of the south-western Cape, South Africa. J Zool (Lond) 209:125–147

DuToit JT, Jarvis JUM, Louw GN (1985) Nutrition and burrowing energetics of the Cape mole-rat *Georychus capensis*. Oecologica 66:81–87

Hartline PH (1971) Physiological basis for detection of sound and vibration in snakes. J Exp Biol 54:349–371

Heth G, Frankenberg E, Raz A, Nevo E (1987) Vibrational communication in subterranean mole rats *(Spalax ehrenbergi)*. Behav Ecol Sociobiol 21:31–33

Honeycutt RL, Edwards SV, Nelson K, Nevo E (1987) Mitochondrial DNA variation and the phylogeny of African mole rats (Rodentia: Bathyergidae). Syst Zool 36:280–292

Honeycutt RL, Nelson K, Schlitter DA, Sherman PW (1991) Genetic variation within and among populations of the naked mole-rat: Evidence from nuclear and mitochondrial genomes. In: Sherman PW, Jarvis JUM, Alexander RD (eds) The biology of the naked mole-rat. Princeton University Press, Princeton New Jersey, pp 195–208

Jarvis JUM (1981) Eusociality in a mammal: Cooperative breeding in naked mole-rat colonies. Science 212:571–573

Jarvis JUM (1991) Reproduction of naked mole-rats. In: Sherman PW, Jarvis JUM, Alexander RD (eds) The biology of the naked mole-rat. Princeton University Press, Princeton New Jersey, pp 384–425

Jarvis JUM, Bennett NC (1991) Ecology and behaviour of the family Bathyergidae. In: Sherman PW, Jarvis JUM, Alexander RD (eds) The biology of the naked mole-rat. Princeton University Press, Princeton New Jersey, pp 66–96

Kenagy GJ (1976) Field observations of male fighting, drumming, and copulation in the Great Basin kangaroo rat, *Dipodomys microps*. J Mammal 57:781–785

Koyama H, Lewis ER, Leverenz EL, Baird RA (1982) Acute seismic sensitivity in the bullfrog ear. Brain Res 250:168–172

Lacey EA, Alexander RD, Braude SH, Sherman PW, Jarvis JUM (1991) An ethogram for the naked mole-rat: Nonvocal behaviours. In: Sherman PW, Jarvis JUM, Alexander RD (eds) The biology of the naked mole-rat. Princeton University Press, Princeton New Jersey, pp 209–242

Lewis ER, Narins PM (1985) Do frogs communicate with seismic signals? Science 227:187–189

Lloyd JE (1973) Model for the mating protocol of synchronously flashing fireflies. Nature 245:268–270

Lloyd JE (1983) Bioluminescence and communication in insects. Annu Rev Entomol 28:131–160

Moore SW, Lewis ER, Narins PM, Lopez PT (1989) The call timing algorithm of the white-lipped frog, *Leptodactylus albilabris*. J Comp Physiol A 164:309–319

Morin JG (1986) Firefleas of the sea: Luminescent signalling in marine ostracode crustaceans. Florida Entomologist 69:105–121

Mueller M, Burda H (1989) Restricted hearing range in a subterranean rodent, *Cryptomys hottentotus*. Naturwissenschaften 76:134–135

Narins PM (1990) Seismic communication in anuran amphibians. Bioscience 40:268–274

Narins PM, Lewis ER (1984) The vertebrate ear as an exquisite seismic sensor. J Acoust Soc Am 76:1384–1387

Pepper JW, Braude SH, Lacey EA, Sherman PW (1991) Vocalization of the naked mole-rat. In: Sherman PW, Jarvis JUM, Alexander RD (eds) The biology of the naked mole-rat. Princeton University Press, Princeton New Jersey, pp 243–274

Rado R, Levi N, Hauser H, Witcher J, Adler N, Intrator N, Wollberg Z, Terkel J (1987) Seismic signalling as a means of communication in a subterranean mammal. Anim Behav 35:1249–1251

Randall JA (1984) Territorial defense and advertisement by foot-drumming in bannertail kangaroo rats *(Dipodomys spectabilis)* at high and low population densities. Behav Ecol Sociobiol 16:11–20

Randall JA (1989) Individual footdrumming signatures in banner-tailed kangaroo rats *Dipodomys spectabilis*. Anim Behav 38:620–630

Reichman OJ, Jarvis JUM (1989) The impact of three species of fossorial herbivorous mole-rats (Rodentia: Bathyergidae) on overlying vegetation. J Mammal 70:763–771

Reichman OJ, Smith S (1990) Burrows and burrowing behavior by mammals. Current Mammal 2:197–244

Reichman OJ, Whitham TG, Ruffner G (1982) Adaptive geometry of burrow spacing in two pocket gopher populations. Ecology 63:687–695

Ross RJ, Smith JJB (1978) Detection of substrate vibrations by salamanders: Inner ear sense organ activity. Can J Zool 56:1156–1162

Rupert A, Moushegian G (1970) Neuronal resonses of kangaroo rat ventral cochlear nucleus to low-frequency tones. Exp Neurol 26:84–102

Sherman PW, Jarvis JUM, Alexander RD (eds) (1991) The biology of the naked mole-rat. Princeton University Press, Princeton, New Jersey

Smithers RHN (1983) The mammals of the southern African subregion. University of Pretoria, Pretoria, Republic of South Africa

Walker EP (1975) Mammals of the world. Third ed. vol II. Baltimore. The Johns Hopkins University Press. i–viii, pp 647–1500

Webster DB, Webster M (1972) Kangaroo rat auditory thresholds before and after middle ear reduction. Brain Behav Evol 5:41–53

Webster DB, Webster M (1980) Morphological adaptations of the ear in the rodent family Heteromyidae. Am Zool 20:247–254