thalamus. The findings strongly suggest that the area controls reproductive activity and may be an important locus for interactions between male and female systems. Studies in other fishes are consistent with the present results in that stimulation of specific thalamic sites elicited sperm release in goldfish and sunfish and light organ discharge, a courtship display, in midshipmen[6].

The thalamus of teleosts is known to receive input from both the retina[8–11] and optic tectum[8] and thus presumably integrates visual information. The anatomy is consistent with a thalamic control of sex-color phases in response to the visual displays of other individuals. In this regard, the brain stimulation could be activating either thalamic afferents or efferents or both simultaneously. Cases where one pattern was evoked during stimulation and another as an after-response could be due to activation of systems which inhibit other systems during stimulation. The after-response is observed as the latter rebound to the inhibition. Confirmation of such mechanisms must await neurophysiological analysis and the relationship of such after-responses to natural behavior is also unknown.

Reproductive activity in sea bass is seasonal and the DP and RV patterns have only been observed during the spawning period[2–4]. The thalamus of some teleosts contains sex-steroid concentrating neurons[12] and gonadotropin-releasing hormone (GnRH)-containing cell bodies and/or axons[13,14]. If such hormone-specific neuronal distributions are also present in sea bass, they could provide substrates for seasonal control of thalamic sensitivity and hence sexual coloration.

Sex-steroid concentrating neurons are also present in the thalamus of jawless fishes, amphibians, reptiles, birds and mammals while GnRH-containing cells or fibers are reported in the area in amphibians and mammals[15]. Electrical stimulation of the caudal intralaminar thalamus in monkeys evokes penile erection and genital scratching[16]. The comparative data extend our hypothesis of sex-hormone modulation of thalamic sensorimotor pathways to mammals and other vertebrates. Such thalamic mechanisms may indeed be primitive features underlying the evolution of the diverse and highly successful reproductive behavior characteristic of vertebrates[17].

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Adaptive optimal sound for vocal communication in tunnels of a subterranean mammal *(Spalax ehrenbergi)*[1]

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Summary. The adaptive value of sound signal characteristics for transmission in the underground tunnel ecotope was tested using tunnels of the solitary territorial subterranean mole rats. We analyzed the propagation of synthetic calls with various frequencies through natural tunnels along different distances. Here we present evidence that sound propagation proved efficient only across short distances (a few meters). The least attenuation of sounds occurred at low frequencies. The 440 Hz sound was transmitted better than the lower (220 Hz) or higher (880, 1760, 3520 Hz) tested frequencies. These characteristics matched perfectly with the mole rat features of vocalization and hearing, thus reflecting the operation of natural selection for adaptive vocal communication in the underground tunnel ecotope.

Key words. Sound transmission underground; vocal communication; subterranean mole rats.

Subterranean rodents exhibit varied degrees of atrophy of eyes and vision and hypertrophy of olfaction and vocal communication[2–6]. Auditory communication is important for existence in the unique underground ecotope and serves a wide range of functions, such as aggression, territoriality[7,8], assortative mating and ethological reproductive isolation[9–11]. The study of vocal communication of subterranean rodents has been conducted to date only in few genera, *Spalacopus*[12], *Talpa*[6,13,14] and *Spalax*[7,11,15], and should be extended. Courtship calls of mole rats *Spalax ehrenbergi* were analyzed recently[15]; they ranged primarily from 500 to 4500 Hz, peaking at around 500 Hz. A study of cochlear microphonics of mole rats (manuscript in preparation) matched the above vocalization data very well. The frequency range was found to be between 0.1 and 8 kHz, with a sensitivity maximum between 0.5 and 1.0 kHz. In addition, recordings of evoked potentials from the inferior colliculus of the mole rat midbrain revealed a sensitivity maximum at around 0.5 kHz. Studies of vocalizations in *Spalacopus*[12], *Talpa*[6,13] and *Spalax*[7,11,15] revealed also low frequency calls. It seems therefore that low frequency calls may characterize both subterranean insectivores and rodents. The adaptive value of calls in a certain habitat should be tested according to their maximal efficiency in

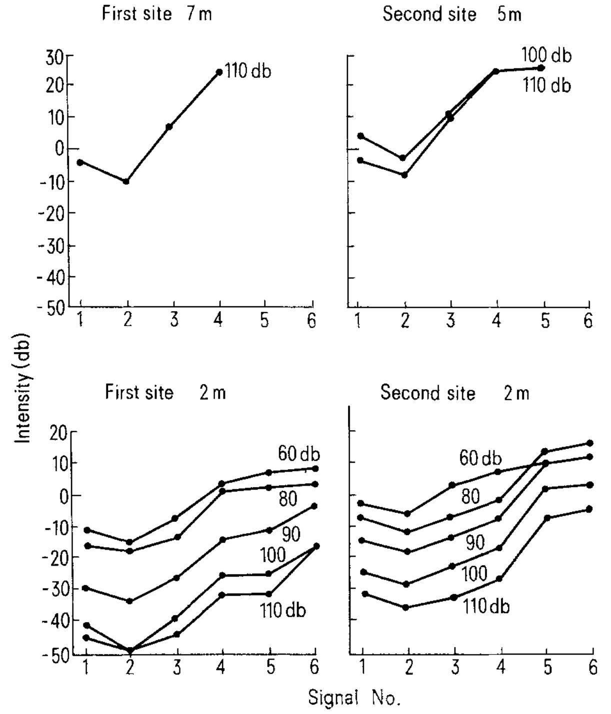

Figure 1. The energy needed to produce a standard sound level of −1 db from the various recordings of signals of different frequencies in different intensities. Each point represents one recording.

transmission through the media[16,17]. Relatively little is known about the acoustic conditions of relevance to animals in terrestrial environments, and the transmission of sounds through underground tunnels has never been studied. We have tested the hypothesis that low spectral peaks are indeed adaptive in underground communication and present here evidence substantiating this hypothesis in mole rats of the *Spalax ehrenbergi* superspecies.

Mole rats are subterranean rodents, completely blind[3], solitary[18] and aggressive[19]. Their sealed burrow system provides a suitable test case for the adaptive transmission of low frequency calls underground.

Materials and methods. A series of 6 notes with different frequencies, each lasting 7 s, were generated by a Commodore 64 Personal Computer and recorded on tape. The 6 signals involved the following frequencies: 1) 220 Hz, 2) 440 Hz, 3) 440 and 880 Hz, with two additional faint harmonic bands at around 1200 and 1600 Hz, 4) 880 and 1760 Hz, 5) 1760 and 3520 Hz and 6) 3520 Hz. The signals could be played back at 5 different intensities of 60, 80, 90, 100 and 110 db, as measured in the air 10 cm from the loudspeaker. A lower intensity than 60 db could not be measured under our conditions, although the mole rat courtship calls measured at the same distance are about 50 db loud. Two Nagra tape recorders were used for playing back the signals and for recording them. Natural tunnels of mole rats at a depth of 15 cm were opened at two ends; the loudspeaker of one recorder was put into one end, and the microphone of the other was inserted into the tunnel through the other. Both tunnel openings were covered to prevent background noises.

Two sites were chosen for testing the transmission of each of the 6 signals played back at the different intensities through the mole rat straight tunnels. The first site was located at Daliyat el karmil, Mount Carmel, in an open field with red terra rossa soil, in which recordings were made from distances of 2 and 7 m from the sound source. The second site was located near the Campus of the University of Haifa on Mount Carmel, in a park forest with light gray rendzina soil. Here recordings were made from distances of 2 and 5 m, according to tunnel availability.

Recordings were analyzed as follows. Each signal was recorded once, at every intensity level. The input level of each recording was noted. Then, the output of the recorder was connected to a potentiometer, measuring intensities in db. The output signal was then increased or reduced, to produce a sound of a standard −1 db intensity. This output level, corrected by the input level used for recording the signals, gave the energy needed to produce the −1 db intensity for each signal. Measurements were made throughout the whole 7 s of each signal. Then all signals were analyzed with a sonagraph model 7030A Kay Vibralizer, at the wide band filter mode, to test the frequencies that remained in the recordings after the transmission of sounds through the tunnels.

Results. The results are represented in figures 1 and 2. At the first site (Daliyat el karmil), from the recordings made at 7 m distance, only the loudest 110-db signals could be analyzed. The other intensities were too weak to be distinguished over the background noise. At 2 m distance, all recordings were measureable. At the second site (University of Haifa), at a distance of 5 m the two loudest (100 and 110 db) intensities recorded were measurable, and at 2 m all intensities were analyzable. The energy needed to produce a signal of −1 db from each recorded signal at the various playback intensities in the four experiments

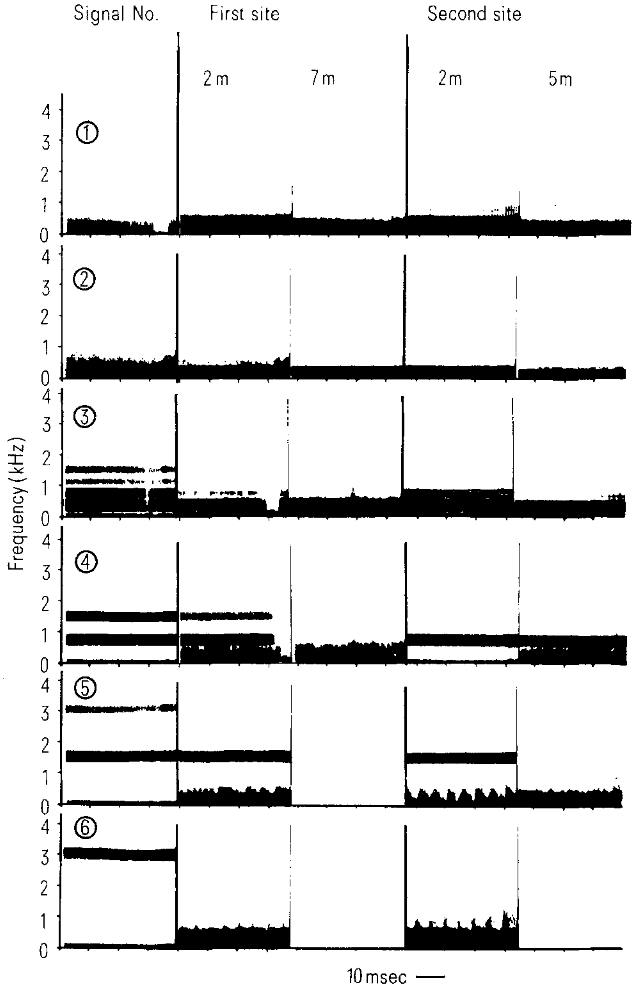

Figure 2. Sonograms of the various playback signals (left side) in comparison to sonograms of their recordings after being transmitted through the underground tunnels. Sound intensity of the presented signals was 110 db. The background noise for signals 1–3 did not exceed 100 Hz, but increased relatively in signals 4–6, since the intensity of the recorded signals decreased with increasing frequency (fig. 1). See 'Material and methods' for explanation.

(two sites and two distances at each) is shown in figure 1. It is clearly seen that in each case the second signal (440 Hz) needed the least energy for transmission through the mole rat tunnel. Consequently we conclude that it is the optimal one of all the signals tested for transmission through the ground. All other signals had to be broadcast at a stronger intensity in order to produce a sound of the same magnitude. The 60 db curve of the second site at 2 m (fig. 1) flattens at points 5 and 6 as a result of a better signal-to-noise ratio in this recordings, compared with the other intensity curves.

The sonograms (fig. 2) show clearly that frequencies higher than 440 Hz were filtered out during the passage of signals through the tunnels. Signals 1 (220 Hz) and 2 (440 Hz) were fully transmitted. In signal 3 only the lowest (440 Hz) frequency was fully transmitted at all distances in the two localities, whereas the frequency of 880 Hz was transmitted only across 2 m distance and faded away at a distance longer than 5 m. For signal 4, 880 Hz was noticeable at a distance of 2 and 5 m but disappeared at 7 m, whereas 1760 Hz was recorded only at the shorter distance in Daliyat el karmil. For signal 5, 1760 Hz was noticeable only at 2 m, whereas 3520 Hz completely disappeared. For signal 6 (3520 Hz) no transmission whatsoever was recorded at any distance.

Discussion. Our results suggest that low frequency sounds are transmitted better than high frequency ones in the air of underground tunnels, for all intensities and distances tested. This is probably because low frequency sounds (consisting of long wavelength) collide less than high frequency ones (short wavelength) with the tunnel walls, and therefore are less absorbed. The 440 Hz frequency was the best transmitted through the tunnel out of all tested frequencies and needed the least energy for transmission, in comparison to either higher (880–3520 Hz) or lower (220 Hz) frequencies. Frequencies higher than 440 Hz are probably more absorbed in the tunnel walls, whereas the lowest tested frequency (220 Hz) seems to be weaker due to reflection from the walls and therefore also less intensely transmitted. These results match well with the main (approximately 500 Hz) frequency of the mole rat courthsip sound[15], with other vocalizations of mole rats[7] and with the hearing ability of mole rats (report in preparation).

The intensity of the mole rat courtship call was found to be about 50 db[15] (approximately the same as the lowest intensity tested here). Signals of that magnitude faded in the present study across a distance of more than 2 m. Considering the efficiency of vocal transmission through the air in the tunnels, it is apparent from the results that acoustical communication of mole rats is efficient only across a short range, i.e. not more than 5 m. Therefore mole rat calls seem not to be effective for longer distances. The distance between individual mole rats is generally large since they live in nature in solitary neighboring territories. A long-range acoustical communication system that exists between mole rats, probably for territorial defence and reproductive functions, may well use other means, such as thumping the head against the ceiling of the tunnel (report in preparation) which produce vibrations transmitted directly through the earth. When confrontation between individuals does occur (for courtship, mating or aggression), it is from a short range. Thus we conclude that the moe rat's low frequency calls, which are most efficient for vocal transmission across short range, are adaptive to communication in underground tunnels and are presumably molded by natural selection.

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On selecting for pupation height in *Drosophila simulans*

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Summary. Selection for high and low pupation height has been carried out in a base *D. simulans* population derived from recently collected isofemale lines. Only the selection for increased pupation height was successful. At generation 8 around 50% of the individuals in the high lines attained the upper end permitted by the apparatus, and selection was stopped. The mean realized heritability was 18%. The finding of additive genetic variation for pupation height in *D. simulans* settles the question posed by a previous failure of selection reported in this species.

Key words. Pupation height; *Drosophila simulans;* directional selection.

The choice of suitable pupation sites by *Drosophila* larvae should be considered as an important fitness component in view of the direct repercussion this behavior has on pupal viability[1]. Genetic control for pupation behavior has been demonstrated in several *Drosophila* species[2–4], and parallelism between field observations and laboratory performance has been noticed recently for some larval patterns of behavior[3]. Strains of *D. melanogaster* quickly responded to selection for pupation height in the upward direc-