

# Preliminary evidence for the use of microseismic cues for navigation by the Namib golden mole

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Insect prey of the Namib golden mole congregate beneath clumps of grass scattered among the sand dunes of the Namib Desert. In the presence of the light winds that typically blow over the Namib Desert, these grass clumps emit low-amplitude vibrations that are transmitted through the sand. While foraging in the sand-swimming mode (a few centimeters below the surface of the sand), some moles apparently were attracted toward manmade sources emitting vibrations matching those recorded from the grass clumps. This is the first direct evidence that these desert mammals use seismic cues for navigation. © 2006 Acoustical Society of America. [DOI: 10.1121/1.2151790]

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## I. INTRODUCTION

There is growing literature on the uses or potential uses of seismic signals (substrate vibrations), especially by arthropods (Autrum and Schneider, 1948; Markl, 1983; Cocroft, 2001) and fossorial mammals (Mason and Narins, 2001; Kimchi and Terkel, 2002), but also by reptiles (Hartline, 1969, 1971; Hetherington, 1989, 1992; Young and Morain, 2002), amphibians (Koyama *et al.*, 1982; Lewis, 1984; Lewis and Narins, 1985; Lewis *et al.*, 2001), and even large land mammals (O'Connell-Rodwell, Hart, and Arnason, 2001). Use of seismic cues for prey localization in sandy habitats has been a productive topic (Brownell, 1977; Brownell and Farley, 1979a, 1979b, 1979c; Hetherington, 1989, 1992; Young and Morain, 2002), and one especially relevant to the work described here.

Among the dunes of the Namib Desert, clumps of dune grass (*Stipagrostis sp.*) or ostrich grass (*Cladoraphis spinosa*) form small, scattered islands on a sea of sand. Beneath these islands, living among the roots of the grass, are dune termites (*Psammotermes sp.*), the principal insect prey of the Namib golden mole (*Eremitalpa granti namibensis*) (Fielden, Perrin, and Hickman, 1990). While foraging for these insects, the mole, which has poorly-developed eyes with fused eyelids (Gubbay, 1956) and cannot form images, takes remarkably straight paths from grass clump to grass clump. These paths frequently span more than ten meters between clumps, and they cover an average distance of approximately 1400 m per night (Fielden *et al.*, 1990; Fielden, 1991; Sey-

mour, Withers, and Weathers, 1998). A previous study, carried out in 1993 near Gobabeb, demonstrated that this foraging is purposeful, not random (Narins *et al.*, 1997). Foraging must, therefore, involve sensory cues (other than vision), even if the animal learns its foraging routes and then reuses them.

Certain golden moles, including *Eremitalpa*, are well-known to have disproportionately large auditory ossicles (Forster Cooper, 1928; von Mayer, O'Brien, and Sarmiento 1995; Mason, 2003b). The combined mass of the malleus and incus in *Eremitalpa* is approximately 0.1% of the animals total body mass, compared to only 0.001% in the comparably-sized laboratory mouse, *Mus musculus*, and only 0.00008% in humans (see Mason, 2001). Several authors have suggested that these hypertrophied ossicles are adaptations for detecting ground vibrations (Kuyper, 1984; Fielden *et al.*, 1990; Hickman, 1990; Narins *et al.*, 1997), perhaps by means of a mechanism referred to as *inertial bone conduction* (Fay and Popper, 1985; Lombard and Hetherington, 1993). Employing a physical model of inertial bone conduction, Mason investigated this possibility further (Mason and Narins, 2002; Mason, 2003a). He concluded that the geometries of the enlarged ossicles of *Eremitalpa* made them especially suitable for the detection of low-frequency ground-borne vibrations of very low amplitude (low-frequency microseismic signals). The golden mole might use this ability in order to navigate, and possibly also to identify and locate prey on or beneath the sand (Narins *et al.*, 1997).

In its natural habitat, E.g., *namibensis* moves either on the surface of the sand or just beneath it with a sand-swimming motion (Meester, 1964; Holm, 1969; Fielden,

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Hickman, and Perrin, 1992). When it is on the surface, the mole stops approximately every 60 cm and dips its head into the sand. As it comes close to a grass clump, its head dips occur closer together (Narins *et al.*, 1997). Head-dipping by desert vertebrates is believed to couple the head more closely to the substrate, aiding in the detection of microseismic signals (Hetherington, 1992; Narins *et al.*, 1997). In the sand-swimming mode of travel, beneath the surface of the sand, the mole's head would be coupled continuously to the substrate. The earlier study at Gobabeb demonstrated that the mole's preferred microhabitats for feeding (clumps of live dune grass) emit distinct microseismic signals whenever there is wind (Narins *et al.*, 1997). Moles typically rest beneath dune-grass clumps when they are not feeding, thus using them for shelter as well. We hypothesized that if *E.g., namibensis* does use microseismic cues for navigation, then it should be attracted to buried artificial seismic sources emitting appropriate signals. We tested this hypothesis with moles released in the presence of seismic transducers emitting the vibration patterns of dune grass clumps in a gentle wind (thus simulating familiar landmarks).

## II. METHODS

We carried out our study on Die Duine Farmstead (25° 14.47' S, 16° 03.39' E), approximately 100 km west of Mal-tahöhe, Namibia, in the NamibRand Nature Reserve. Approximately 1 km from the farmstead buildings, we selected a flat area of sand, clear of grass clumps and approximately 20 m in diameter, at the center of which we planted a small clump of ostrich grass (*Cladoraphis spinosa*). We established an experimental arena as the area inside a circle, 10 m in diameter and centered on the clump of ostrich grass. Around the perimeter of the arena we deployed eight seismic sources at 45° intervals, beginning at a position 22.5° east of north (i.e., north-northeast) relative to the center of the arena. These sources (Clarke Synthesis transducers, model TST 229 F4 ABS) were disk-shaped, 21 cm in diameter and were buried approximately 30 cm below the surface of the sand. For each source, a uniquely labeled coaxial cable was laid outside the arena. The cables were buried approximately 10 cm beneath the surface of the sand, and extended to a small table approximately 5 m beyond the edge of the arena and west-northwest from the arena's center. A vertical geophone (OYO Geo Space GS-20DX, damped with a 1-k $\Omega$  resistor) was buried to a mean depth of approximately 4 cm near the center of the arena, on the side of the ostrich-grass clump closest to the table. Its coaxial cable was buried approximately 15 cm below the surface of the sand and led directly through the arena to the table. The geophone cable was connected to a high-gain, low-noise amplifier (constructed from National Semiconductor LF441 ACH operational amplifiers), the output of which was connected to one input channel of a battery-operated oscilloscope (Sony/Tektronix 305).

The signal for driving the seismic sources was synthesized digitally and recorded as a 16-bit wave file on a compact disk (CD). It comprised 60 s of bandlimited Gaussian noise, the amplitude spectrum of which had been sculpted to match the difference spectrum from the earlier Gobabeb re-

cordings [Narins *et al.*, 1997, Fig. 5(b)]. This was the difference between the amplitude spectrum of the seismic noise recorded (in a gentle wind) from the sand immediately adjacent to dune-grass clumps and that of the seismic noise recorded simultaneously in open areas at least 20 m away. In our last two experiments, we used the same noise pattern with randomly-timed click waveforms added to it. We had recorded these clicks from a vertical geophone buried to a mean depth of approximately 4 cm at the edge of an ostrich-grass clump approximately 200 m west of the arena. Because the clicks occurred near only a small fraction of the ostrich-grass clumps that we sampled, we surmised that they were emissions from potential prey items (e.g., insects) of the mole. The stimulus CD was played from a portable CD player (Classic CL413), with a track repeat feature. Thus the 60-s track was repeated with almost seamless transitions for many hours. The selected output channel (right or left) of the CD player was connected to both input channels (right and left) of a stereo power amplifier (Road Gear RGCA 100) and to a single input channel of a second, identical amplifier. Each of the corresponding outputs was connected through one of the buried coaxial cables to a single seismic source at the perimeter of the arena.

For each experimental trial, three neighboring sources were activated; the other five sources were silent. The amplitude of each source was adjusted to yield approximately 0.0001 cm/s (root-mean-square vertical velocity) at the geophone at the center of the arena. Within the arena, the vibration field established by this excitation pattern could be divided into two regions of approximately equal areas. In one region the stimulus vibration amplitude (from the active sources) was greater than that at the point at which each mole was released; in the other region it was less than that at the release point. The trio of sources to be made active was varied randomly from trial to trial. At the adjusted vibrational level, the air-borne sound level, measured 0.5 m from the surface of the sand directly above each source was approximately 36 dB SPL. The vibrational stimulus spectrum was centered at approximately 350 Hz [see Fig. 5(b) in Narins *et al.*, 1997]. Evidently owing to frequency-dependent coupling from sand to air, the spectrum of the corresponding airborne sound was centered at a lower frequency, approximately 240 Hz. We recorded airborne sound emitted by a *Stipagrostis* clump in a gentle breeze and found that its power was concentrated between 35 and 90 Hz, with much reduced levels above 100 Hz.

For each trial, once the source amplitudes had been adjusted, a single mole was released at approximately the same position (the west-southwest edge of the ostrich-grass clump at the center of the arena). Upon release, the mole immediately burrowed into the sand near or beneath the clump and remained there for several hours. The investigators then withdrew as quietly as possible, to the farmstead buildings in most cases. In those cases, the mole's activity was checked periodically by a single observer approaching the arena stealthily. In a few cases, one or two investigators remained behind, sitting very quietly at a distance of more than 50 m from the arena. From there, the mole's activity was observed through binoculars. In every trial, the path that the mole had

TABLE I. Basic information is given about each of the eleven moles, numbered in order of release. Neither the sex nor the weight of mole 1 was determined before its release. GMT is Greenwich Mean Time.

Mole number	Date caught	Sex	Mass (g)	Date, local time (GMT+3) of release
1	Sep 01, 2002	...	...	Sep 01, 1703 h
2	Aug 30, 2002	M	20	Sep 02, 1158 h
3	Aug 31, 2002	M	25	Sep 02, 1920 h
4	Aug 31, 2002	F	18	Sep 03, 1235 h
5	Aug 31, 2002	M	22	Sep 03, 2258 h
6	Aug 31, 2002	M	26	Sep 06, 1130 h
7	Aug 31, 2002	F	15.5	Sep 07, 1210 h
8	Sep 07, 2002	F	19	Sep 08, 1043 h
9	Sep 07, 2002	F	16.5	Sep 09, 1347 h
10	Sep 07, 2002	F	19	Sep 12, 1530 h
11	Sep 08, 2002	M	19.5	Sep 13, 1610 h

taken was easily seen. Once the mole had exited the arena and left the vicinity, its track was mapped in a piecewise-linear fashion. The heading of each track segment was measured (with a string or a narrow-beam light) relative to the arena perimeter, and the length of each segment was measured. Preparation for the subsequent trial included thorough raking of the sand, down to approximately 10 cm, to erase the previous mole's tracks and to disperse any scent-trail it may have left.

Eleven moles were available for this project (see Table I); each was used only once and subsequently returned to the wild. While in captivity, the moles were housed in 20-liter

plastic buckets containing dune sand and were provided with mealworms (tenebrionid larvae) and local termites ad lib.

### III. RESULTS

The results for all eleven moles are presented in Figs. 1–4, which show the mole tracks superimposed on the vibration field computed (on the basis of two-dimensional power spread) for the corresponding trio of active sources. The right-hand panel of Fig. 4 shows the orientation of the arena, determined by GPS observations, in each of the other panels in Figs. 1–4. The axes are labeled in meters from the center of the arena. The large outer circle represents the perimeter of the arena; the small, inner circle represents the ostrich grass clump (approximately to scale). The sources are depicted as small circles (filled with black and drawn to scale) distributed along the large outer circle. Solid line segments (gray or black) represent track segments made by sand-swimming moles; dotted line segments represent track segments made by moles walking on the surface. Taking geophone measurements at 32 points distributed uniformly in azimuth ( $45^\circ$  apart) and radial distance from the center of the arena (1.0 m apart), we corroborated and calibrated the computed vibration field map to within 1.0 m of the active sources. The contour lines in Figs. 1–4, calibrated in this manner, are separated by 4 dB. In each figure, note the second innermost contour line surrounding all three active sources (about half way from the arena center to the centermost active source). This line corresponds to the vibration amplitude measured next to live dune-grass clumps under conditions of light wind

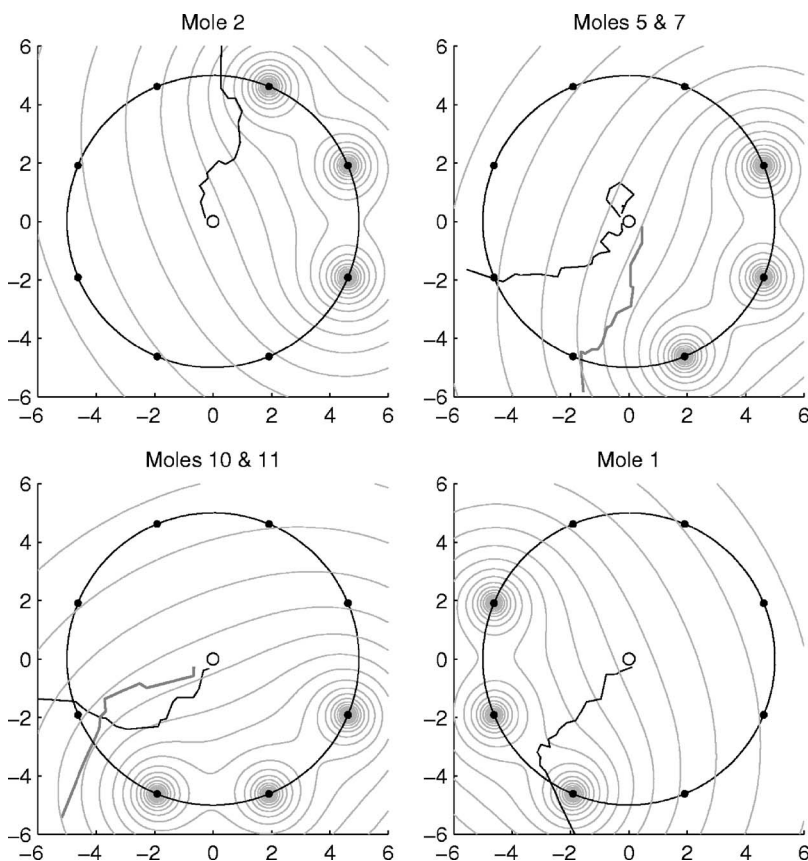


FIG. 1. Tracks of six sand-swimming moles. The axes are labeled in meters from the center of the arena. Computed contours of constant vertical-vibration amplitude are depicted in pale gray. At locations within the arena that are greater than 1.0 m from any active source, the calibrated contour spacing is 4 dB. Compass directions are given in the right-hand panel of Fig. 4. In each panel, true north is up and east is to the right. The tracks of moles 5 and 11 are depicted in dark gray, those of moles 7 and 10 in black.

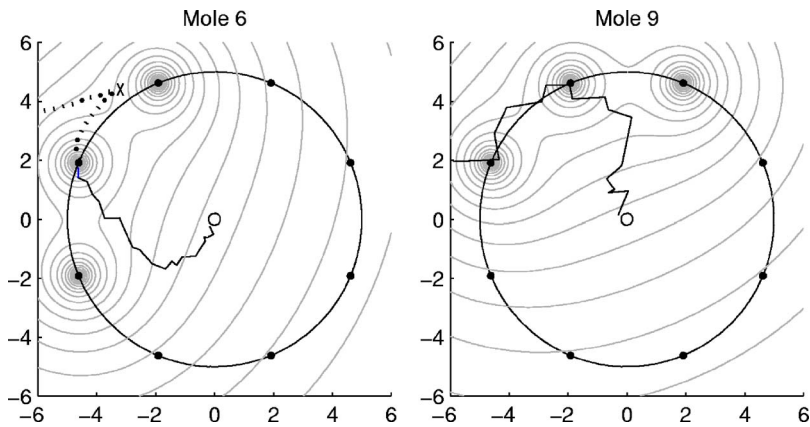


FIG. 2. Tracks of moles 6 and 9. The solid black line segments represent sand-swimming tracks. The dotted line segments represent surface-walking tracks. The final approach of mole 6 to the source in the west-northwest position was a dive, too deep to leave a track on the surface. Axes, contours, and arena orientation are the same as in Fig. 1.

(wind velocity near 0 m/s at ground level to approximately 3 m/s at 2 m above the ground) (Narins *et al.*, 1997).

For each of the eleven moles, the time between its release and its subsequent journey out of the arena ranged from 2 to 20 h. We intended to present the stimulus continuously during that time. Occasionally, however, we were required to interrupt the stimulus briefly in order to replace nearly-spent batteries. Each power amplifier was powered by a pair of rechargeable, 12-V lead-acid batteries. As long as the battery voltage exceeded approximately 10 V, the amplifier performance was unchanged. When the voltage fell below that level, the amplifier shut down completely. On each visit to the arena, we checked the batteries with a voltmeter and replaced them as needed. On only one occasion (mole number 4 in Table I) did an amplifier shut down during an experiment. During a visit to the arena, the observer found that the mole had not begun to move and that the amplifiers still were functioning. On the subsequent visit, 75 min later, he found that the mole had left the arena area and that the amplifier driving the source at north-northwest and the source at north-northeast had shut down (see Fig. 4). Because we were unsure of the point at which failure had occurred, we eliminated this mole from consideration in our acoustical results. To avoid failure of the portable CD player, the dry cells powering it were replaced on a regular schedule. In only one instance (mole number 6 in Table I) did the player fail prematurely. On one visit to the arena, the observer found that the mole had moved approximately 2 m along its track toward the arena perimeter and that all three sources were functioning. On the subsequent visit, 100 min later, he found

that the mole had left the arena area and that the CD player (driving all three sources) had shut down. The point at which failure occurred seemed to be indicated by an abrupt course reversal (marked by X in the left-hand panel of Fig. 2). Furthermore, the mole's conspicuous behavior in the vicinity of the west-northwest source (see below) strongly suggested that, as it approached the source, it was aware of the source's presence. Therefore, we included this mole in our statistical analysis. The reader should remain aware of the potential bias in this decision and feel free to treat the results from both moles 4 and 6 as he or she sees fit.

By the time we were ready to use moles 10 and 11 (our last two moles), we had noticed that moles tended to go directly over the active sources when they were distributed along the northwestern quadrant of the perimeter. No moles had been enticed to exit even close to active sources along the southeastern quadrant. For that reason, we tried twice more to draw the moles in the southeastern direction, adding putative prey sounds to enhance the attractiveness of the stimulus.

Most of the track plots are self-explanatory. The plots for moles 6 and 9 warrant elaboration, however. The track of mole 6 not only exited the arena at an active source (the west-northwest source), but in the final approach to that source, this mole dove toward the center of the source. The mole then resurfaced (to normal sand-swimming depth) and circled the perimeter of the source, which was buried at least 20 cm below the mole's body. After circling the source, it immediately emerged to walk on the surface, heading first toward a neighboring source (which was or had been active),

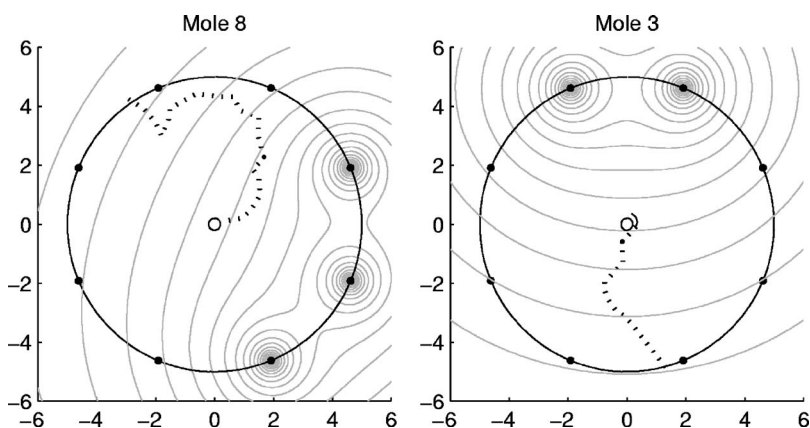


FIG. 3. Tracks of two surface-walking moles. In the case of mole 3, the third source was inadvertently disconnected from its power amplifier. Axes, contours, and arena orientation are the same as in Fig. 1.

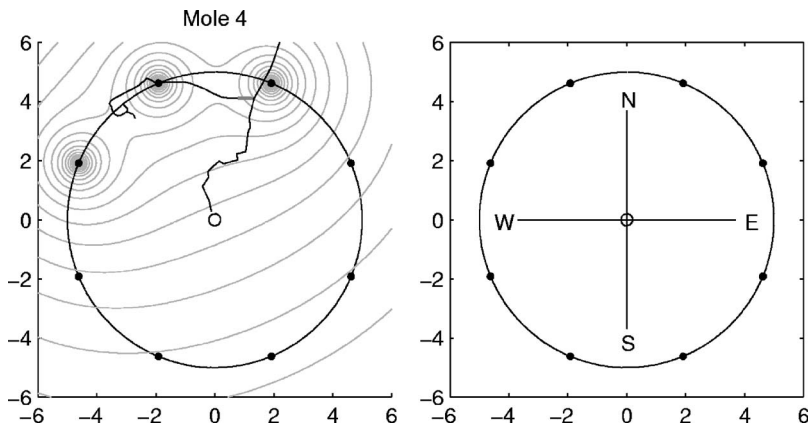


FIG. 4. (Left panel) Sand-swimming tracks of mole 4. The westward detour began with a dive (denoted by the dark gray segment), leaving no surface track. The contours show the position of the stimulus field prior to battery failure. (Right panel) Compass directions for all panels in Figs. 1–4.

then abruptly reversing direction (at the position marked by X) and heading westward, away from the arena. Mole 9 exited the arena directly over an active source, then turned westward along the arena perimeter, reentered the arena and exited again, over the neighboring active source. Then, continuing to sandswim, it headed westward, away from the arena.

#### IV. DISCUSSION

##### A. Implications regarding the use of acoustic cues

Among the ten moles counted in this study (excluding mole 4), only two (moles 6 and 9) exited the arena directly over an active source. Consider each mole to be a trial, and take its first exiting from the arena directly over an active source to be a success (a hit) and first exiting the arena anywhere else a failure (a miss). Assume, as a null hypothesis, that all points around the arena perimeter are equally likely to be the mole's point of first exit, even in the presence of the vibratory stimuli. In that case, the probability that any given trial would lead to a hit (in the presence of three active sources, each of diameter 21 cm on a perimeter with 5-m radius) is given by

$$p = (3 \times 0.21) / (2\pi \times 5) = 0.0201.$$

The probability that none of the ten trials results in a hit is given by

$$(1 - p)^{10} = 0.8166.$$

The probability that the ten trials would lead to exactly one hit is given by

$$10p(1 - p)^9 = 0.1671.$$

Therefore, the probability ( $P$ ) of more than one hit in ten trials (our outcome) under this null hypothesis is

$$P = 1 - 0.8166 - 0.1671 = 0.0163.$$

This value of  $P$  gives us slightly better than 98% confidence that our outcome would not be the result of chance under the first null hypothesis. In other words, when the targets are tiny, as they are here, even two hits out of ten trials can be significant.

We cannot be sure, however, that there was no pre-existing bias (independent of source position) influencing the mole's exit point from the arena. Regardless of the position

(or absence, possibly, in the case of mole 4) of the active sources, none of the 11 moles exited over the south-southeast source or the north-northeast source, or over the eastern perimeter segment lying between those two sources. This was the side of the arena facing the edge of the dune fields. Extended for approximately 100 m, a path out of this part of the perimeter would carry a mole beyond the dunes, onto a vast gravel plane. The eight sources divide our arena perimeter into an ordered set of eight segments. No exit points occurred along three contiguous members of that set. Under our first null hypothesis, the probability that, after 11 trials, there remains, somewhere along the perimeter, a subset of three or more contiguous segments in which no exit points have occurred is 0.042 (see Appendix). Thus there is reason to believe that our first null hypothesis is inappropriate. A bias toward the west would increase the probability of hitting a target by chance, and thus possibly reduce the significance of the hits by moles 6 and 9. It is appropriate, therefore, to re-evaluate the chance occurrences under an alternative null hypothesis; that exiting anywhere along the perimeter segment between and including the four east-side sources has an *a priori* probability of zero, and that all points along the remaining perimeter segment are equally likely to be the mole's first point of exit.

Under this second null hypothesis, moles 2, 5, 7, and 8 had no targets at all in the acceptable region. Moles 3, 10, and 11 each had one target in the acceptable region. Mole 9 had two targets in the acceptable region, and moles 1 and 6 each had three targets in the acceptable region. In other words, the ten trials are reduced to six. The probability that any of the three trials involving moles 3, 10, or 11 would lead to a hit is given by

$$p = p_1 = 0.21 / ((5/8) \times 2\pi \times 5) = 0.0107.$$

For the trial involving mole 9

$$p = p_2 = (2 \times 0.21) / ((5/8) \times 2\pi \times 5) = 0.0214.$$

For the two trials involving moles 1 or 6

$$p = p_3 = (3 \times 0.21) / ((5/8) \times 2\pi \times 5) = 0.0321.$$

The probability that none of the six trials would produce a hit is given by

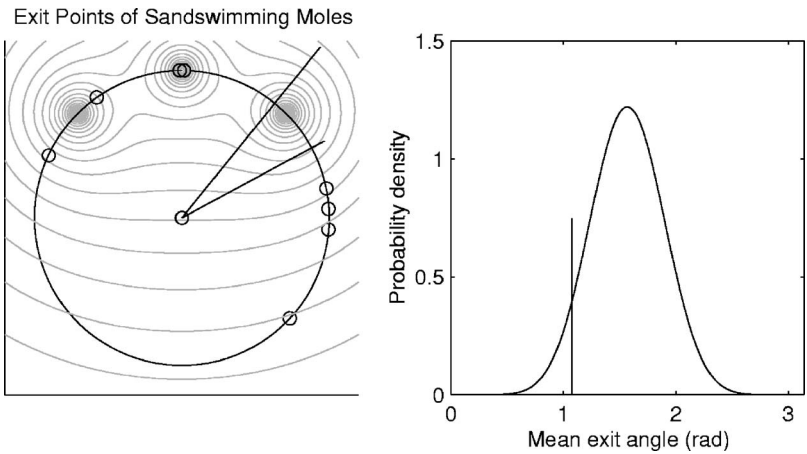


FIG. 5. (Left panel) The arena is depicted with the central active source at the top. Open circles depict the first points at which the eight sand-swimming moles exited the arena relative to the location of that source. Treating each exit point as a unit radial vector relative to an origin at the center of the arena, one can compute a vector sum (whose direction is depicted by the longer of the two radial lines). The magnitude of the vector sum is 3.51. Taking the null hypothesis to be uniform *a priori* probability distribution for each unit vector over the  $-\pi$  to  $\pi$  rad of possible directions ( $\theta$ ) relative to that of the central source, one would apply the Rayleigh test. In this case, the statistic  $Z$  for the Rayleigh test has the value of 1.54. This corresponds to a  $P$  value of approximately 0.21. With eight trials, for a  $P$  value of 0.05 or less,  $Z$  would need to be 2.9 or more, corresponding to a vector-sum magnitude of 4.85 or more. The same null hypothesis can be translated to a uniform *a priori* distribution (from 0 to  $\pi$ ) of absolute directions ( $\text{abs}[\theta]$ ) relative to the direction of the central source. The shorter of the two radial lines shows the direction of the mean absolute direction (mean exit angle). (Right panel) The mean exit angle (1.0765 rad) plotted against the probability density function (unit=1.0  $\text{rad}^{-1}$ ) computed for eight trials under the null hypothesis. In this case, the  $P$  value for the data is 0.063.

$$(1 - p_1)^3(1 - p_2)(1 - p_3)^2 = 0.8877.$$

The probability that they would produce exactly one hit is given by

$$(3p_1)(1 - p_1)^2(1 - p_2)(1 - p_3)^2 + (1 - p_1)^3(p_2)(1 - p_3)^2 + (1 - p_1)^3(1 - p_2)(2p_3)(1 - p_3) = 0.1070.$$

Therefore, the probability ( $P$ ) of more than one hit in the six trials (our outcome) under the second null hypothesis is

$$P = 1 - 0.8877 - 0.1073 = 0.0053.$$

This value of  $P$  gives us slightly better than 99% confidence that our outcome would not be the result of chance under the second null hypothesis. Thus the westward bias suggested by the data does not reduce the significance of the two direct hits on west-side targets.

Among the eight trials (excluding mole 4) in which the moles traveled out of the arena predominantly in the sand-swimming mode, the choice of a northerly or southerly direction appears to be correlated with the location of the trio of active sources. This was true even when the active sources were located along the (possibly unacceptable) eastern 3/8 of the arena perimeter. When the majority of active sources was located along the northern half of the perimeter, the moles ( $N=3$ ) exited there; when the majority was located along the southern half, the moles ( $N=5$ ) exited there. On the other hand, under the first null hypothesis (all exit points around the perimeter equally likely), a more objective assessment of directional tendency is provided by circular statistics (see Fig. 5). For both vector sum and mean angle, the data fail to reach the 95% confidence level, although the mean angle is close, at  $P=0.063$ . It was the failure of these statistics that led us to focus on the apparent successes with moles 6 and 9, and to the wording of the title of this paper. Nonetheless, owing to the small target size, the analysis in the previous paragraph tells us that the direct hits by moles 6 and

9 provide compelling evidence in favor of the hypothesis embedded in the title. This conclusion is bolstered by the second direct hit by mole 9, which was not included in our analysis.

The surface-walking moles (3 and 8) clearly were not attracted to the active seismic sources. This might be attributable to the spectral difference between the airborne sound emitted from the sand surface over our active seismic sources and the airborne sound emitted by *Stipagrostis* (the simulated vibrations from which we were using as stimuli). While the seismic stimulus components matched the *Stipagrostis* vibrational spectrum, the airborne stimulus components may have seemed alien to the mole subjects. The two surface-walking moles periodically head-dipped and thus were exposed to both the seismic and airborne components. While sand-swimming, on the other hand, the remaining eight moles were exposed only to the seismic component.

## B. Implications regarding nonaural cues

The trail of mole 4 (left-hand panel of Fig. 4) branched twice and ended abruptly at two points (the sources that were active prior to battery failure are depicted in the figure). The trail began near the central clump of ostrich grass and eventually exited the arena close to the source at the north-northeast location. After exiting, it continued down the side of the ridge and off into a field of ostrich-grass clumps. Before exiting at that point, the mole took a long westward detour—along a route that passed directly over the source in the north-northwest position, then re-entered the arena and branched (northwest of the arena center) to form two blind ends. The mole clearly passed this branch point at least twice. Thus it was able to retrace at least part of its original path. It also must have passed the first branch point (north-northeast of the arena center) at least twice. It seems likely that the mole retraced the entire detour, bringing it back pre-

cisely to the original route. At least two cues could be available for this: (1) the topography of the sand surface along the trail, and (2) a scent-trail.

Near the beginning of its trail, mole 4 seems to have followed closely the route of mole 2, made approximately 24 h earlier. After it was measured and recorded, the trail of mole 2 had been raked thoroughly, and the wind subsequently had smoothed the surface of the sand. Nevertheless, it seems possible that mole 4 was attracted to a scent trail (or some other cues) left behind by mole 2. One sees a similar coincidence of the initial parts of the routes of moles 6 (male) and 10 (female). The laying down of those two trails was, however, separated by 6 days and at least two thorough rakings (of the trails of mole 6 and the trail of mole 7). Furthermore, other moles released in the arena during these six days did not follow the route of mole 6. The use of a scent-trail therefore seems unlikely.

For navigation in the absence of microseismic signals (e.g., under windless conditions, no nearby prey) golden moles presumably use nonaural cues, possibly based on tactile, olfactory, or even magnetic senses (Kimchi and Terkel, 2001). The apparent aversion of the sand-swimming moles to easterly routes may have resulted, in part, from a tendency of moles to follow routes close to those of their predecessors, utilizing such nonaural cues. On the other hand, moles 6 and 9 diverged strongly from the routes of their predecessors, taking routes directly toward active sources in the northwest quadrant. It should be noted that the arena was within a hundred meters of the eastern edge of the dune fields. An easterly path therefore, if continued, would take a mole out of its habitat.

### C. Directional sensitivity

The results with moles 6 and 9 suggest that these moles were not only attracted toward the active sources, but were able to determine the directions of those sources. While in the sand-swimming mode, these moles were exposed to substrate-borne vibration but not (directly) to airborne sound. Mason and Narins (2002) briefly discussed three hypotheses for directional sensitivity to vibratory stimuli: (1) Use of interaural time or phase difference in the propagating seismic wave; (2) Directional sensitivity potentially imparted by a pushed-up ridge of sand acting as a seismic lens for surface-walking moles; (3) The localization potential of having non-parallel axes of rotation of the middle-ear ossicles. Use of interaural time or phase difference would require that a substantial component of the vibration imparted to the right-hand side of the mole's skull be independent of that imparted to the left side (i.e., that the skull not vibrate entirely as a unit). Such independence of motion awaits verification. The second hypothesis presumably would not apply to our sand-swimming moles. Here we expand on hypothesis 3.

Vertical particle motion, by itself, carries no information about the direction of the source. Such information would be carried, however, by a horizontal component of particle velocity that is aligned with the direction of seismic-wave propagation. In sand, seismic waves are propagated as surface (Rayleigh) waves or compressional ( $P$ ) waves

(Brownell, 1977). Appropriate horizontal particle-velocity components are present in both. At low frequencies, however, horizontal propagation of  $P$ -waves in sand may not be possible (Liu and Nagel, 1992). The vertical geophone in the arena monitored the vertical particle velocity component of the Rayleigh wave. The conduction velocity of Rayleigh waves in loose sand is approximately 40–50 m/s (Brownell, 1977), yielding a wavelength of approximately 80–100 cm at 500 Hz and greater than that for lower frequencies. The particles in a Rayleigh wave follow elliptical paths (for a graphical demonstration, see Russell, 2001). Within two-tenths of a wavelength of the surface, the horizontal motion at the top of the ellipse is directed toward the source; at the bottom of the ellipse it is directed away from the source. Below that depth, the elliptical motion is reversed. The sand-swimming moles were within 16 cm of the surface, making them well within two-tenths of a wavelength for the spectral components of our stimuli. By trial-and-error, seeking the direction of greatest stimulation, the mole could utilize the horizontal particle motion monaurally. The radiographs featured in Forster Cooper (1928) and Gasc, Jouffroy and Renous (1986) suggest that the axes of rotation of the mole's right and left ossicular chains are not parallel to each other in the horizontal plane. If that is so, then obliquely incident horizontal particle motion would excite the two ossicular chains to different extents, and the difference would bear information regarding source direction. This could allow binaural localization of the seismic source, an intriguing possibility that awaits experimental verification.

## V. CONCLUSIONS

Statistical analysis of the data suggests, with only 93% confidence, that the paths of all eight sand-swimming were influenced by the vibratory fields generated by those sources. With confidences of 98% or 99% (depending on our choice of null hypothesis), on the other hand, the results imply that the paths of two of the eight sand-swimming moles were purposefully directed toward active sources, and that those two moles therefore must have used the sources as navigational beacons.

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## APPENDIX: CALCULATION OF PROBABILITY

In this study, none of the eleven moles exited over the easterly 3/8 of the arena perimeter. In order to establish the likelihood that this was a chance occurrence, rather than the result of a westerly bias, we undertook the following analysis. Take the eight sources to divide the arena perimeter into a set of eight nonoverlapping segments of equal length, so that the first exit point of each mole can be assigned unambiguously to one of the eight. Assume that the *a priori* probability of its lying in a given segment is 1/8. Before the first trial, there are eight (overlapping) subsets that comprise three contiguous segments. After the first trial, three of those subsets are removed as candidates for the putative excluded zone. Unless they all produce first exit points in the same segment as the first, subsequent trials will reduce further the number of candidates. The goal here is to compute the probability that the number of candidates will be reduced to zero at or before the end of the eleventh trial. This can be accomplished by means of a seven-state Markov chain with the following stochastic projection matrix:

$$\mathbf{A} = [\mathbf{p}_5; \mathbf{p}_4; \mathbf{p}_3; \mathbf{p}_{2b}; \mathbf{p}_{2a}; \mathbf{p}_1; \mathbf{p}_0]$$

$$\mathbf{p}_5 = [1/8, 1/4, 1/4, 1/4, 1/8, 0, 0]$$

$$\mathbf{p}_4 = [0, 1/4, 1/4, 1/4, 0, 1/4, 0]$$

$$\mathbf{p}_3 = [0, 0, 3/8, 1/4, 0, 1/4, 1/8]$$

$$\mathbf{p}_{2b} = [0, 0, 0, 1/2, 0, 1/4, 1/4]$$

$$\mathbf{p}_{2a} = [0, 0, 0, 0, 1/4, 3/4, 0]$$

$$\mathbf{p}_1 = [0, 0, 0, 0, 0, 5/8, 3/8]$$

$$\mathbf{p}_0 = [0, 0, 0, 0, 0, 0, 1].$$

This matrix operates on the vector  $\mathbf{P}(n)$ ,

$$\mathbf{P}(n) = [P_5(n), P_4(n), P_3(n), P_{2b}(n), P_{2a}(n), P_1(n), P_0(n)],$$

where  $P_m(n)$  is the probability that  $m$  three-segment candidates remain after  $n$  trials (there are two distinct states with two candidates remaining). Defining

$$\mathbf{P}(1) = [1, 0, 0, 0, 0, 0, 0],$$

one can carry the operation  $\mathbf{A} \cdot \mathbf{P}$  through ten steps to compute  $P_0(11)$ . The probability that at least one candidate is left after 11 trials is its complement,  $1 - P_0(11)$ .

$$P_0(11) = 0.958,$$

$$1 - P_0(11) = 0.042.$$

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