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DECODING THE TUNNEL BEHAVIOR OF DAMARALAND MOLE-RATS
(*FUKOMYS DAMARENSIS*)

by

Cristina Aurora Rodriguez-Wagner

A Thesis

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Abstract

Damaraland mole-rats, *Fukomys damarensis*, are an African rodent species that is one of the two mammalian species considered eusocial. Damaraland mole-rats (DMR) live in large colonies comprised of a breeding pair and their non-reproductive offspring in underground tunnel systems. Many adaptations in DMR could be traced back to either their eusocial or subterranean lifestyle. DMR exhibit a behavior within their tunnels that consists of undulating their bodies, reminiscent of a break-dance move. The goal of this research was to characterize the properties of this enigmatic behavior. First, we investigated who exhibited the behavior and found that DMR break-dance regardless of age and sex, but breeding status played a role. Second, we investigated what sensory stimuli elicit break-dancing and found the behavior is elicited by vibrations and air currents in breach simulations, suggesting this behavior is stimulated by specific sensory inputs rather than by general arousal to all environmental stimuli.

Preface

One of the research goals of the Freeman lab is to identify neuroendocrine and behavioral mechanisms that characterize eusocial mammals, particularly the Damaraland mole-rat (*Fukomys damarensis*). Damaraland mole-rats (DMR) are one of two mammalian species generally accepted as eusocial because they reside in colonies with up to 40 individuals, consisting of a dominant breeding female (often referred to as a queen), her mate, and their non-reproductive offspring. The eusocial mating system is more commonly seen in insect species such as bees, ants, and wasps. DMR also live their entire lives underground in tunnel systems in the semi-arid region of southwest Africa. These factors have led to unique physiological, anatomical, and behavioral adaptations to not only the eusocial lifestyle but also to the challenges of the subterranean environment. One enigmatic behavior that DMR exhibit is a tunnel behavior that consists of the undulation of the entire body, resembling a break-dance move we have called “the worm.” To our knowledge, this behavior has yet to be formally studied. Hence, the focus of my thesis was to lay the groundwork for the break-dancing behavior. This included identifying which individuals in the colony exhibited the behavior and what sensory stimuli elicited the behavior.

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Chapter 1: Introduction

The subterranean environment poses many challenges for fossorial mammalian species, especially in terms of sensory ecology. The constant darkness coupled with the reduction of odors' ability to travel makes locating food, mates, family members, or intruders difficult (Heth and Todrank 2007). Not only is the use of sight and smell restricted, but hearing is impaired as well since airborne sounds propagate poorly through the substrate, limiting communication via vocalization to only short distances within tunnel systems (Heth, Frankenberg, and Nevo 1986).

Mole-rats, a group of highly fossorial rodent species, have adapted to the constrained sensory information of the underground environment. As a result of the subterranean life, mole-rat species have poor vision and small eyes with corneas that are sensitive to air currents (Eloff 1958). In addition, their hearing abilities are limited, having lost the ability to hear high frequency sounds (Heffner and Heffner 1992); (Bruckmann and Burda 1997). They are however still sensitive to lower frequencies, which travel better through substrate compared to higher frequencies (Heffner and Heffner 1992); (Bruckmann and Burda 1997).

Subterranean rodents have had to employ different channels of communication than above ground rodents. Drumming behavior is widely observed as a form of signaling to conspecifics in mole-rats and contains both auditory and vibratory (seismic) components (Mason and Narins 2001). Social mole-rats exhibit drumming behaviors when in close proximity to one another, such as foot drumming in both mating displays and signaling to a resting conspecific to move (Bennett and Jarvis 1988); (Bennett 1990). As for long distance communication, generation of seismic signals, or vibrations through the soil, has appeared in multiple solitary mole-rat species. For example, blind mole rats, *Spalax ehrenbergi*, signal territory and burrow occupancy by repeatedly thumping their heads on the roof of the tunnel (Rado, Terkel, and

Wollberg 1998). Demon African mole-rats, *Tachyoryctes daemon*, also produce seismic signals by drumming their head on the roof of the tunnel and produce two signals that vary in speed under different circumstances, indicating that the signals convey different information (Hrouzková et al. 2013). Cape mole-rats, *Georychus capensis*, have been found to use seismic signals through foot drumming to communicate the sender's sex and reproductive condition in an effort to find potential mates in neighboring burrow systems (Narins et al. 1992).

Like other mole-rat species, Damaraland mole-rats (DMR), *Fukomys damarensis*, are highly fossorial and spend most if not their entire lives underground in deep permanent tunnel systems (Thomas, Swanepoel, and Bennett 2016) in the semi-arid region of southwest Africa. DMR are one of two mammalian species generally considered eusocial, the other being naked mole-rats (*Heterocephalus glaber*). The hallmarks of eusociality are overlapping generations and a clear division of labor (Thomas et al. 2016). Damaraland mole-rats reside in colonies with up to 40 individuals (Kelley et al. 2019) that consist of a breeding pair and their non-reproductive offspring that engage in work, such as foraging, maintaining the burrow system, and nest building (Bennett and Jarvis 1988).

Not only do Damaraland mole-rats have a rare social system, but they also exhibit a tunnel behavior that consists of the undulation of the entire body, resembling a break-dance move called “the worm.” There are few anecdotes that seem to describe this behavior, along with presumptions as to the function of the behavior. For instance, one claim involves Damaraland mole-rats flattening their bodies and moving up and down in an S-shaped fashion to force air along the tunnels and communicate to colony members through these air pulse signals (Wood and Mendez n.d.). Another anecdote describes a pumping behavior seen in common mole-rats, *Cryptomys hottentotus*, that sounds remarkably similar to break-dancing wherein these animals

flatten their bodies and repeatedly lift and lower their hindquarters (Eloff 1958). In this case, researchers speculated that the mole-rats perform this behavior to aid in sensing air currents caused by breaches in the tunnel system, thus allowing them to find the origin of the air current and repair it (Eloff 1958).

On the other hand, break-dancing may be DMR's version of seismic signaling. It is possible that DMR are producing vibrations when their hindquarters strike of the roof the tunnel. There are many examples of mole-rat species found to use seismic communication. In addition, broad patterns have been established for subterranean rodents, in that solitary species tend to use seismic signals for long distance communication, while social species primarily use vocalizations since they are generally in close proximity to conspecifics (Francescoli 2000). Despite these patterns, seismic signaling is not necessarily out of the realm of possibilities for DMR. Large colonies of Damaraland mole-rats occupy larger burrow systems that cover great areas (Thomas et al. 2016). Therefore, there is potentially a need for longer distance communication in large colonies of Damaraland mole-rats.

As far as we know, the break-dancing behavior had yet to be studied. Thus, foundational knowledge of this behavior needed to be established. First, in an observational study, we characterized which individuals in colonies exhibit this behavior. Second, we determined the sensory stimuli that elicit the break-dancing behavior in DMRs to begin narrowing down the possible functional significance of the behavior.

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Chapter 2: Characterizing the Formal Properties of the Break-dancing Tunnel

Behavior in Damaraland Mole-rats (*Fukomys damarensis*)

Abstract

Damaraland mole-rats (DMR) are a subterranean rodent species that is regarded as eusocial. Many adaptations in DMR can be understood in light of their subterranean and eusocial lifestyles. DMR exhibit a break-dancing behavior in their tunnel systems that has yet to be formally examined. The goal of this research was to characterize the properties of this behavior by investigating whether there are age, sex, or social status-dependent aspects of the behavior. We found that the behavior was expressed at all ages examined and in both males and females. However, breeders almost never exhibited the behavior compared to non-breeders, indicating that there is a social status component to the behavior.

Keywords: Damaraland mole-rats, eusocial, underground, subterranean, behavior

Introduction

The study of animal communication is essential in gaining a more comprehensive understanding of a species because it sheds light on both the social environment and sensory capabilities of a species (Francescoli 2000). Communication among subterranean species has become of interest because of the sensory challenges these species face due to their underground environment. They are a fascinating example of how signaling is influenced not only by the sensory capabilities of individuals, but also by the physical conditions of the environment (Francescoli 2000). The constant darkness renders any visual signals useless. In addition, chemical and auditory signals, such as vocalizations, are constrained to within tunnels due to the signals' poor propagation through substrate (Heth and Todrank 2007); (Heth et al. 1986).

Mole-rats, a diverse group of subterranean rodents, have developed behavioral mechanisms in response to the sensory challenges of the subterranean environment. Drumming behavior is widely observed as a form of signaling to conspecifics in mole-rats and contains both auditory and vibratory (seismic) components (Mason and Narins 2001). Social mole-rats use the auditory component of drumming as a signal in situations where they are in close proximity (Bennett and Jarvis 1988);(Bennett 1990). Multiple solitary species have utilized the vibrations produced from drumming their heads or feet on tunnel walls for communication, such as blind mole rats (*Spalax ehrenbergi*), Demon African mole-rats (*Tachyoryctes daemon*), and Cape mole-rats (*Georychus capensis*) (Rado et al. 1998); (Hrouzková et al. 2013);(Narins et al. 1992). Seismic signaling is important because it appears to be the only form of long-distance communication that subterranean species have that travel beyond the boundaries of their tunnels.

Damaraland mole-rats (DMR), *Fukomys damarensis*, are a subterranean rodent species that are endemic to southwest Africa. They are one of two mammal species generally regarded as eusocial, the other species being the naked mole-rat (*Heterocephalus glaber*). Eusociality is a breeding system more commonly found among insects such as ants, bees, and wasps (Wilson 1971). As a eusocial species, Damaraland mole-rats form colonies with up to 40 individuals of overlapping generations with clear division of labor (Kelley et al. 2019; Thomas et al. 2016). Colonies are comprised of a dominant breeding female, up to two breeding males, and the breeding individuals' non-reproductive offspring, who carry out duties for the colony such as foraging, maintaining the burrow system, colony defense, and nest building (Bennett and Jarvis 1988). Colony tunnel systems include deep permanent burrows and shallower foraging tunnels (Thomas et al. 2016) that DMR excavate in search for tubers, a primary component of their diet.

DMR have unique morphological, physiological, and behavioral adaptations as a result of their eusocial and fossorial lifestyle. For instance, DMR have poor visual acuity and small external eyes with corneas that are sensitive to air currents due to living in the darkness of the subterranean environment (Eloff 1958). Dominant females drum their feet during courtships with the dominant male (Bennett and Jarvis 1988). In addition, dominant females have elongated bodies compared to subordinate females, which is likely an adaptation to fit within the burrows while pregnant and bear more offspring (Young and Bennett 2010). Subordinate females do not undergo puberty as long as they remain in their natal colony (Bennett and Jarvis 2004).

DMR exhibit a novel behavior in tunnels that as far as we know has not been formally studied. The behavior consists of the undulation of the entire body, resembling a break-dance move called “the worm.” The mole-rat’s hindquarters often hit the roof of the tunnel when it break-dances, meaning it could be a drumming signal. It is important to investigate this behavior because if it is a form of communication, it will shed more light on the social environment of this eusocial species. Little is known about the behavior, such as which individuals in the colony exhibit the behavior or its function, or whether it is an adaptation to being fossorial or eusocial. The aim of this study was to characterize the formal properties of the break-dancing behavior, in particular, which individuals exhibit the behavior? Thus, we focused on determining if there is a sex component to the break-dancing behavior, an age component to the break-dancing behavior, or a social status (breeder vs non-breeder) component to the break-dancing behavior.

Materials and Methods

Animals and Housing

Damaraland mole-rat colonies observed in this study are housed at the University of Memphis. They are fed sweet potatoes ad libitum with supplements of dry rodent pellets (Harlan 2019, 19% protein diet). Rooms were held on a 16:8 light/dark cycle (light onset 7:00). Each colony is housed within complex structures that can consist of two different sized cages (60x40x20cm and 48x25x20cm) and are connected by varying lengths of extruded polycarbonate tubing to simulate natural burrow architecture. The number of cages and length of tube are dependent on the size of the colony. For this study, eight colonies with tubes measured 40cm or longer were observed. The colonies totaled 87 mole-rats, 28 females and 59 males of 11 were breeders; ages ranged from 1 to 16 years.

Observations

Eight colonies were observed beginning November 2019 through the end of January 2020. In total there were 23 observations between the hours of 7:00 and 15:00, each lasting approximately one hour. For identification purposes, each adult mole rat has a subcutaneous transponder with unique ID number. In the event that a mole-rat exhibits the break-dancing behavior, the observer used an AVID microchip scanner to scan the mole rat's transponder and recorded their ID number. The AVID microchip scanner is able to scan through the plastic tube, thereby not disturbing the break-dancer nor the rest of the colony in the scanning process.

After observations were complete, an excel file with colony records was consulted. For any given colony, the records contained information such as the number of individuals in the colony, each of their ID numbers, their birth dates, their social status (breeder or nonbreeder),

and their sex. Observed break dancers' ID numbers were searched in the records to determine information such as the ages, social statuses, and sexes of the break dancers.

The difference in two proportions test statistic was used to analyze if there was a difference in the proportion of individuals that exhibited the break-dancing behavior between females and males and breeders and non-breeders. In addition, a Fisher's exact test was performed to determine if there was an association between age and exhibiting the break-dancing behavior.

Results

In the 8 colonies that were observed, there was a total of 87 mole-rats, of which 42 exhibited the break-dancing behavior at least once during observations. Half (14/28) of the females were observed break-dancing, whereas 47% (28/59) of male mole-rats exhibited the break-dancing behavior (Table 1, Figure 1). The proportions of break-dancing individuals were not significantly different between males and females (p-value = 0.83).

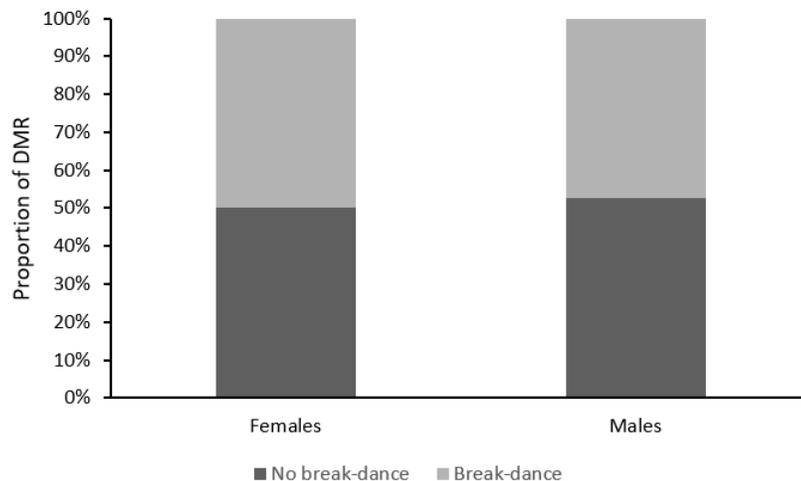


Figure 1. The proportion of each sex that was observed break-dancing and those who were not observed break-dancing among all DMR colonies in the study. Proportion of break-dancing individuals were not significantly different between the sexes (p-value = 0.83).

With respect to breeders, 2 of 11(18%) exhibited the break-dancing behavior, both of which were males (Table 2). In contrast, 53% of the non-breeders exhibited the behavior (40/76). The proportions of individuals exhibiting the behavior differed significantly between breeders and non-breeders (p-value= 0.01).

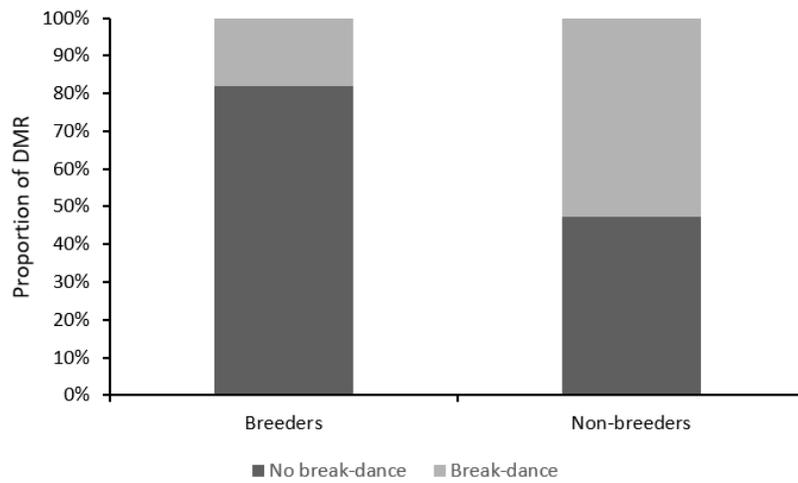


Figure 2. The proportion of each social status that was observed break-dancing and those who were not observed break-dancing among all DMR colonies in the study. Proportion of break-dancing individuals were significantly different between the social statuses (p-value= 0.0067)

The ages of the mole-rats ranged between 1 to 16 years old. A majority of the mole-rats that exhibited break-dancing were at the age of 8 or under (Table 3). However, a large portion of the observed colonies were made up of individuals 8 years old and younger. Age was not as significant factor associated with the break-dancing behavior (p-value= 0.0731).

Colony Number	Females	Males	Females observed BD	Males observed BD
3-093	4	10	3	3
605	5	6	2	2
768	5	8	3	5
785	3	5	3	3
808	6	8	1	5
842	1	10	0	6
845	1	7	1	0
884	3	5	1	4
Total	28	59	14	28

Table 1. Breakdown of distribution of the sexes between all of the colonies and how many of each sex was observed break-dancing vs. was not observed break-dancing. BD refers to break-dancing.

Colony Number	Breeders	Non-breeders	Breeders observed BD	Non-breeders observed BD
3-093	2	12	0	6
605	2	9	0	4
768	2	11	0	8
785	1	7	1	5
808	2	12	1	5
842	1	10	0	6
845	1	7	0	1
884	0	8	0	5
Total	11	76	2	40

Table 2. Breakdown of distribution of the breeders and non-breeders between all of the colonies and how many of each social status was observed break-dancing vs. was not observed break-dancing. BD refers to break-dancing.

	Observed BD	Was not observed BD	Total
Ages 1-4	19	17	36
Ages 5-8	18	12	30
Ages 9-12	4	11	15
Ages 13-16	1	5	6
Total	42	45	87

Table 3. Age groups among all of the colonies and the number of each group that was observed break-dancing or was not observed break-dancing. BD refers to break-dancing.

Discussion

Overall, there was no significant impact of sex or age on the break-dancing behavior. This fits with numerous other observations that indicate little sexual differentiation in DMR (Anyan et al. 2011). Mole-rats of all ages exhibited the behavior with no significant difference among age groups. This finding also aligns with prior findings indicating that DMR have long lifespans and do not senesce, physiologically or behaviorally, as quickly as other mammals of their size (Dammann and Burda 2007). Interestingly, the expression of this behavior did appear to depend on social status, as nonbreeders were significantly more likely to express the behavior as compared to the breeding individuals.

The finding that social status may play a role in exhibiting the behavior further differentiates the castes of breeders from non-breeding “helpers”. These findings extend prior work indicating that there is little neural sexual differentiation in DMR between males and females, although significant neural differences have been found between breeders and nonbreeders (Anyan et al. 2011). It is worth noting that no female breeders were ever observed break-dancing. This may be due to female breeders being morphologically different from other colony members in that their bodies are elongated (Young and Bennett 2010), thus affecting their ability to break dance.

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Chapter 3: Identifying Sensory Stimuli that Elicit the Break-dancing Tunnel Behavior in Damaraland Mole-rats (*Fukomys damarensis*)

Abstract

Two defining characteristics of the Damaraland mole-rats (DMR) are their eusocial mating system and their subterranean lifestyle. As a subterranean species, they have evolved mechanisms to address sensory challenges of underground life. Within their tunnel systems, DMR exhibit a break-dancing behavior that consists of them undulating their bodies. The purpose of this study was to investigate the role of sensory stimuli in eliciting the break-dancing behavior. Mole-rats were placed in five sensory test conditions to determine which stimuli elicited the behavior. We found that the break-dancing behavior is elicited by vibrations and air currents under simulated breach conditions. These findings indicate that this behavior is stimulated by specific sensory inputs, rather than by general arousal in response to all environmental stimuli.

Keywords: Damaraland mole-rats, eusocial, underground, subterranean, sense, sensory stimuli, behavior

Introduction

Damaraland mole-rats, *Fukomys damarensis*, are a unique subterranean rodent species with a rare mating system. They are one of two mammalian species generally accepted as a eusocial species, the other being the naked mole-rat (*Heterocephalus glaber*). Damaraland mole-rats (DMR) fit the criteria of eusociality in that they reside in colonies with up to 40 individuals comprised of a dominant breeding female, her mate, and the breeding pair's non-reproductive offspring (Kelley et al. 2019). In addition to the overlapping generations in colonies that

hallmarks eusociality, there is also a clear division of labor among the colony members (Thomas et al. 2016). DMR colonies excavate their own tunnel systems, which include deep permanent burrows and shallower foraging tunnels (Thomas et al. 2016). They spend most, if not their entire lives underground within their natal colony.

Many anatomical, physiological, and behavioral adaptations in DMR can be traced back to either their eusocial and subterranean lifestyle or both. As a subterranean species, they have evolved mechanisms to address the sensory challenges of underground life because the subterranean environment provides limited sensory information to its inhabitants. Due to the constant darkness, DMR, along with other mole-rat species, have poor vision and small eyes that are sensitive to air currents (Eloff 1958). In addition, the darkness and the poor ability for chemical signals to travel through substrate have made locating food, mates, family members, or intruders from a distance a challenge for subterranean species (Heth and Todrank 2007). Living in large colonies has allowed DMR to ameliorate the challenge of locating food substances. By foraging in groups, DMR have increased their foraging efficiency (Thomas et al) since the number of colony members increases the chance that one of them will find food. Lastly, airborne sounds propagate poorly through substrate, limiting communication via vocalization to only short distances within tunnel systems (Heth et al. 1986). Lower frequency sounds propagate better than higher frequency sounds in the tunnel systems (Heth et al. 1986). Hence, mole-rat hearing sensitivity is restricted to lower frequencies around 1000 Hz (Bruckmann and Burda 1997) (Heffner and Heffner 1992).

However, there are gaps in the understanding of an enigmatic behavior DMR exhibit within their tunnel systems. This behavior has been coined break-dancing because it consists of the mole-rat undulating its body, reminiscent of the break-dance move “the worm.”

There are anecdotal descriptions of this behavior, along with presumptions as to the function of the behavior. For instance, one claim involves Damaraland mole-rats flattening their bodies and moving up and down in an S shaped fashion to force air along the tunnels and communicate to colony members through these air pulse signals (Wood and Mendez n.d.). Another anecdote describes a pumping behavior seen in common mole-rats, *Cryptomys hottentotus*, that sounds remarkably similar to break-dancing wherein this mole-rat species flatten their body and repeatedly lift and lower their hindquarters (Eloff 1958). In this case, researchers speculate that the mole-rats perform this behavior to aid in sensing air currents caused by breaches in the tunnel system, allowing them to find the origin of the air current and repair it (Eloff 1958). Both these hypotheses indicate that DMR may break-dance in response air movement, whether is it is to send an air pulse signal back to the sender or locate a breach.

It is possible that DMR are producing thumping sounds or vibrations when their hindquarters strike of the roof the tunnel. Some fossorial species use seismic communication, vibrations that travel through substrate; in fact, many examples can be found in mole-rat species. Drumming behavior is widely observed as a form of signaling to conspecifics and contains both auditory and vibratory (seismic) components (Mason and Narins 2001). Social mole-rats exhibit foot drumming behaviors in scenarios where they are in close proximity to one another, such as mating displays and signaling to a resting conspecific to move (Bennett and Jarvis 1988)(Bennett 1990). As for long distance communication, generation of seismic signals has appeared in multiple solitary mole-rat species. Blind mole rats, *Spalax ehrenbergi*, signal territory and burrow occupancy by repeatedly thumping their heads on the roof of the tunnel (Rado et al. 1998). Demon African mole-rats, *Tachyoryctes daemon*, also produce seismic signals by drumming their head on the roof of the tunnel and produce two signals that vary in speed under

different circumstances, indicating that the signals convey different information (Hrouzková et al. 2013). Cape mole-rats, *Georychus capensis*, have been found to use seismic signals through foot drumming to communicate the sender's sex and reproductive condition in an effort to find potential mates in neighboring burrow systems (Narins et al. 1992). It is possible that DMR could have a sensitivity to vibrations. Fossorial mammals that use either their heads or incisors for digging are among the best documented cases of seismic sensitivity and communication, most likely due to their heads being close to the substrate at some point in the digging cycle (Mason and Narins 2001). Since DMR use their incisors to excavate, we can hypothesize that they may have a sensitivity to vibrations.

All of these hypotheses of the possible function of the break-dancing behavior involve different sensory stimuli. In addition, airborne sounds and odors are possible external stimuli that elicit the behavior in DMR. Lacking image-forming vision, DMR rely on other sensory modalities to gain information about their environment, thus, odors can be important and could potentially elicit DMR to break-dance. Therefore, in the present study, we investigated the role of several sensory stimuli in eliciting the break-dancing behavior in DMR.

General Methods

Animals and Housing

Damaraland mole-rats used for this study are from colonies housed at the University of Memphis. They are fed sweet potatoes ad libitum with supplements of dry rodent pellets (Harlan 2019, 19% protein diet). Each colony is housed within complex structures that are comprised of different sized cages (60x40x20cm and 48x25x20cm) that are connected by varying lengths of

extruded polycarbonate tubing to simulate natural burrow architecture. The number of cages and length of tubes are dependent on the size of the colony.

For this study, 40 non-breeding mole-rats from various colonies were randomly selected for the experiment. The age of test subjects ranged from 2 to 14 years old. There were 20 females and 20 males. The 40 mole-rats selected for the experiment were divided into 5 groups, each consisting of 8 mole-rats.

General Test Arena

The testing arena was comprised of two cages (34x22x26cm) that were connected by an extruded polycarbonate tunnel measuring approximately 52 cm in length. Minor changes were made to the testing arena to accommodate for each stimulus test condition (details below). Two Yi Lite cameras on tripods were set up at different distances from the test arena. The closer camera focused on the tube, while the farther camera had a full view of the test arena. All stimulus tests were recorded on the two cameras. A white backdrop was constructed to facilitate recognition of the mole-rats for the EthoVision software (see below).

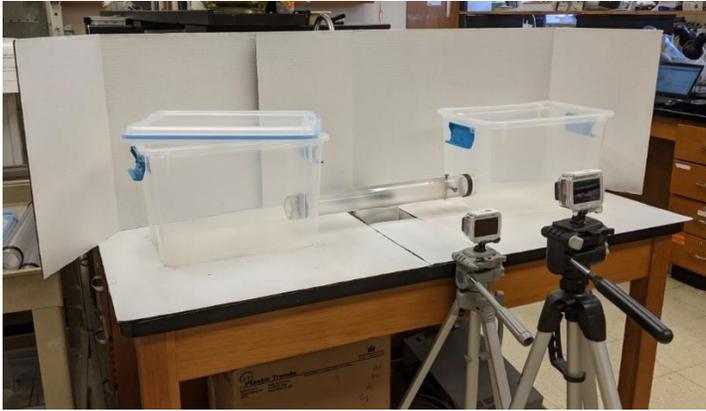


Figure 1. General set up for the testing arena that was modified for each stimulus test conditions. Testing arena comprised of two cages (left is cage A and right is cage B) connected by an extruded polycarbonate tube, and white backdrop. Two Yi cameras were placed at different distances to record trials.

General Procedure

Five stimulus test conditions were designed with the goal that each test condition delivers a single stimulus type to the test subject. The five stimuli were air pulse, sound, breach, odor, and vibration. Overall, the procedure of each test included a 20-minute habituation period for test subject, the sensory stimulus, and then a 5-minute post stimulus period. More detailed procedures for each of the stimulus tests are described below. Each group was scheduled to complete the five stimulus tests in different orders. Mole-rats participated in a stimulus test individually and only once a week to allow them to recover from any minor stress from the stimulus tests and/or being separated from their colony. Stimulus tests were conducted from February 8th to March 29th, 2021 between the hours of 8:00 and 16:00.

Analysis

EthoVision, a video tracking software, was used to analyze and detect when break-dancing occurred and counted undulations. The software was programmed to consider the mole-rat

break-dancing when it met certain parameters such as acceleration, activity levels, velocity, and its rear reaching the roof of the tube during an undulation. To check the accuracy of EthoVison, 25 videos were randomly selected, 5 of each test condition from each of the groups, for the experimenter to review and tally the number of break-dance undulations seen. Then, R^2 was calculated to determine how well the number of undulations the software counted vs what the experimenter counted correlated (see Results).

Break-dancing undulations per min before and after the sensory stimuli were analyzed by Repeated Measures ANOVA. Latency of the expression of break-dancing after the stimuli were delivered was analyzed by One-Way ANOVA. Differences were considered significant if $p \leq 0.05$.

Air Pulse Stimulus Test: Method

Test arena

The test arena consisted of two cages, cage A and cage B. The tube connecting the two cages was fitted with two spokes that crossed at the end of the tube near cage B. Thus, when the test subject was placed in cage A, it was able to enter the tube, but the spokes prevented it from entering cage B. This allowed the experimenter to safely reach their hand in cage B.

To deliver the air pulse stimuli, tubing was attached to an air nozzle. The tubing was able to reach the end of the tube in cage B. An anemometer (Velocicalc air velocity meter, model 9565) was used to measure the draft rate of the air.

Procedure

The test subject was placed in cage A and given a 20-minute habituation period. After the habituation period, an air nozzle was turned on with an average draft rate of 3.04 m/s (STD ± 0.55). The experimenter held the air tube in cage B, pointing it at the entrance of the tunnel connecting the cages. The experimenter pulsed the air with their thumb for 3 seconds. The air tube was removed from the cage for 30 seconds, and then brought back to the tunnel opening and the air was pulsed for 3 more seconds. This process is repeated for 2 minutes, totaling 5 times that the air pulse stimulus is delivered down the tunnel to the test subject. Finally, the test subject was given a 5-minute post stimulus period.

Auditory stimulus test: Method

Test arena

A speaker was placed 1m away from the test arena. The speaker was set to play a 1000 Hz tone. Cages A and B were placed on thin rubber mats to reduce vibrations caused by the speaker. The tube connecting the cages had no alterations and test subject was free to move between the cages.

Procedure

The test subject was randomly placed in one of the cages and given a 20-minute habituation period. After the habituation period, a 1000 Hz tone was played for 3 seconds, every 30 seconds, for 2 minutes. The tone was played a total of 5 times. Afterwards, the test subject was given a 5-minute post stimulus period.

Breach stimulus test: Method

Test arena

To simulate a breach event in a tunnel system, the cages had lids lined with foam padding and could be clamped down to prevent as little air flow as possible in and out of the cages. In addition, a small hole was drilled into the tube closer to cage B and covered with tape. To deliver the air current stimulus, tubing attached to an air nozzle was used. An anemometer (Velocicalc air velocity meter, model 9565) was used to measure the draft rate of the air.

Procedure

The test subject was randomly placed in one of the cages. After the 20-minute habituation period, the tape covering the hole was removed and an air nozzle was turned on with an average draft rate of 2.65 m/s (STD \pm 0.35). The air tube was held at the small hole for 2 minutes. Afterwards, the air nozzle was turned off, the hole was covered with tape again, and the test subject was given a 5-minute post stimulus period before being removed from the test arena.

Odor stimulus test: Method

Test arena

The test arena consisted of two cages, cage A and cage B. The tube connecting the two cages was fitted with two spokes that crossed at the end of the tube near cage B. Thus, when the test subject was placed in cage A, it was able to enter the tube, but the spokes prevented it from entering cage B. This allowed the experimenter to safely reach their hand in cage B and place an odor stimulant. Lids with foam padding were used to keep the odor in the cages.

There were two odor treatments, vanilla extract and soiled bedding, along with distilled water as a control treatment. Vanilla extract was chosen as a novel odor treatment since it is unlikely DMR would have come across that smell in nature or in the animal facility. As a xenophobic species, scents from non-colony members could be of interest to DMR, hence soiled bedding and paper towels were collected from other colonies' cages to be used as an odor stimulus. The odor stimuli were prepared by adding a couple drops of distilled water or vanilla extract on Wattman paper on glass plates. The soiled bedding was poured onto a glass plate.

Procedure

The test subject was placed in cage A and given a 20-minute habituation period. After the habituation period, the odor stimuli and control were given in a random order. One of the odor stimuli or control was placed in cage B near the entrance of the tunnel and the lid was closed for two minutes. The odor stimulus or control was then removed from the cage and the lid is left off to let the cages air out for 5 minutes. This process was repeated (5 minutes between stimuli) with the other two treatments.

Vibratory stimulus test: Method

Test arena

To deliver a vibration stimulus, a Maxi mix II type 37600 Mixer was situated so that the moving plate made contact with the tube connecting the cages when it was turned on. Cages A and B were placed on thin rubber mats and had 200g weights on the side opposite the test tube vortex to reduce the cages from sliding away from the test tube vortex due to the impact. The tube connecting the cages allowed the test subject to freely move between the cages. A digital vibration meter (AS63D vibration meter) measured the displacement.

Procedure

The test subject was randomly placed either in cage A or B and given a 20-minute habituation period. After the habituation period, the test tube vortex vibrated the tube for 3 seconds, every 30 seconds for 2 minutes. In total, the vibration stimulus was delivered 5 times. The average displacement the test tube vortex delivered to the tube was of 0.029 mm (STD ± 0.005). The test subject was given a 5-minute post stimulus period before being removed from the test arena.

Results

EthoVision Accuracy

The correlation between how many undulations EthoVision counted vs what the experimenter counted was found to be $R^2 = 0.73$, meaning that the correlation between EthoVision and the experimenter's counts were moderately strong. Thus, we used EthoVision's data for this experiment. In checking the accuracy of EthoVision, the experimenter carefully watched 25 trial videos. Another conclusion that can be drawn from the videos is that break-dancing only occurs in tunnels, and not in the open space of cages.

Stimulus tests

There was a significant treatment effect on undulations per minute pre- and post-stimulus during the breach and vibration stimulus tests. In the simulated breach test conditions, 23 mole-rats exhibited the behavior after the air current was delivered. The mole-rats performed significantly more undulations after the breach stimulus as compared to before (1.59 vs 0.74 undulations/min, respectively; ANOVA $p=0.01$; Figure 2). Among the 16 mole-rats that expressed the behavior following the vibration stimulus the mean average significantly increased

from 1.31 undulations/min to mean average of 4.88 undulations/min (ANOVA $p=0.03$; Figure 2).

The number of undulations per minute did not differ pre- and post- stimulus with regard to the air pulse, auditory, and odor stimulus tests. During the air pulse stimulus test conditions, 20 mole-rats exhibited the behavior after the air pulses, but undulations/min did not differ significantly before and after the air pulse stimuli were delivered (ANOVA $p=0.13$). Average undulation/min pre- and post- stimulus were 3.90 and 5.88 respectively (Figure 2). As for auditory stimulus test conditions, 11 mole-rats were recorded break-dancing after the tone was played. The average undulation/min prior to the auditory stimulus was 2.12, while post-auditory stimulus the average decreased to 1.48 break-dancing undulation/min (Figure 2). However, this difference was not significant (ANOVA $p=0.54$). Lastly, 12 mole-rats exhibited the behavior after exposure to water on Wattman paper, while 12 and 14 mole-rats exhibited the behavior after the vanilla extract and bedding odor stimuli were placed in the cage, respectively. Break-dancing undulations/min did not differ significantly before and after the first odor stimulus was introduced (ANOVA $p=0.09$). The average undulations/min pre- and post- odor stimulus were 1.33 and 2.63 respectively (Figure 2).

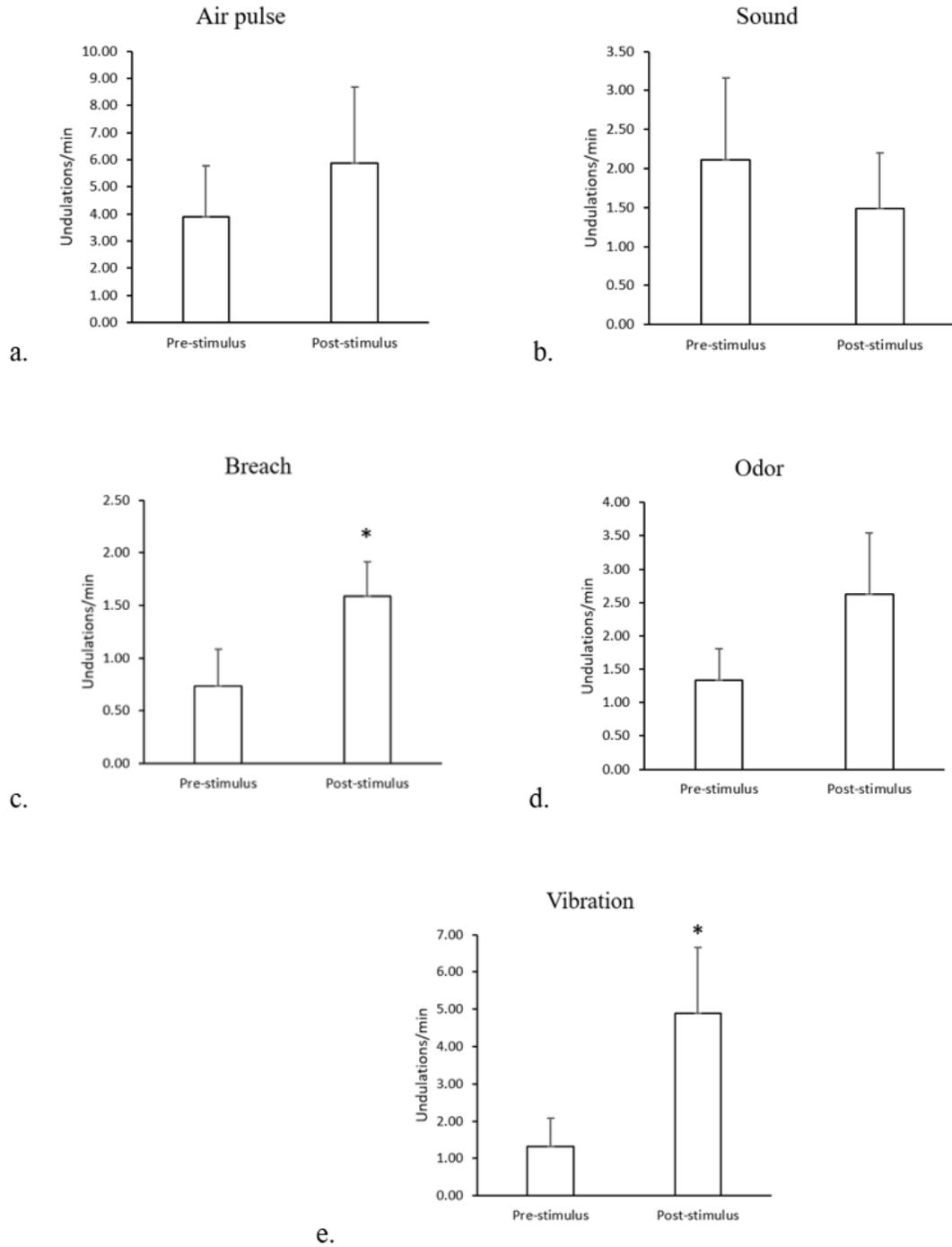


Figure 2. Mean undulations/min (± 1 SE) before and after stimuli. The following graphs: a. Air pulse, b. Sound, c. Breach, d. Odor (all treatments combined) and e. Vibrations. (*) denotes significant difference in undulations/min between pre- and post- stimulus periods.

For those mole-rats that exhibited the behavior following a stimulus, the latency to onset of the behavior relative to the onset of each stimulus did not differ significantly (Repeated Measures ANOVA $p=0.87$; Figure 3).

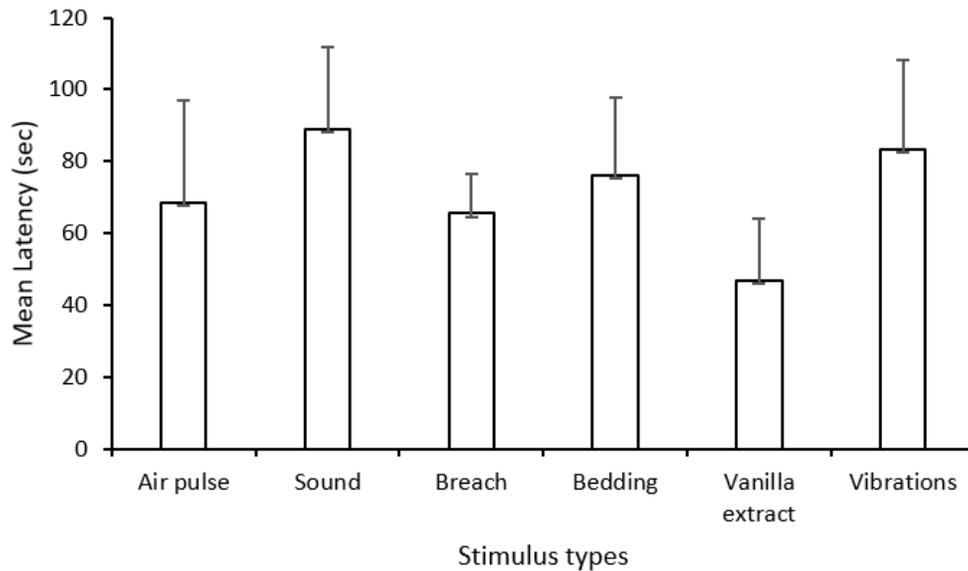


Figure 3. Mean (± 1 SE) latency of the expression of break-dancing after stimulus delivery in seconds. No significant differences between types of stimulus.

Discussion

Our results suggest that the break-dancing behavior is stimulated by specific sensory input, rather than by general arousal in response to all environmental stimuli. In the experiment, the break-dance behavior increased following exposure to a simulated tunnel breach as well as vibration of the tunnel, but not to other stimuli. The pumping behavior described to locate breaches described in common mole-rats (Eloff 1958) is likely the most similar to the break-

dancing behavior in DMR. Considering that break-dancing in DMR significantly increased in a simulated breach scenario, these may represent the same behavior with similar function.

Interestingly, the rate of break-dancing significantly increased after vibratory stimuli as well. These findings suggest that they may use the break-dancing behavior as a form of seismic communication, which defies the broad patterns found in subterranean rodent communication. In general, solitary species tend to use seismic signals for long distance communication, while social species primarily use vocalizations since they are generally in close proximity to conspecifics (Francescoli 2000). However, large colonies of Damaraland mole-rats occupy larger burrow systems that cover greater areas (Thomas et al. 2016). Therefore, there is potentially a need for longer distance communication in large colonies of Damaraland mole-rats.

During the habituation period of the trials, mole-rats exhibited the behavior even though “no stimulus” was being delivered. This may be due to being placed in a new environment that included novel odors and noises that were beyond the experimenter’s control. But if break-dancing is a form of long-distance communication, it is possible that the mole-rats were attempting to communicate with their colony since they were removed from their colony for the day of their group’s stimulus trials.

Even though it was not significant, it is worth noting that the auditory stimulus was the only stimulus that elicited a decrease in break-dancing undulations per minute. DMR are very sensitive to disturbances, including loud sounds. For example, closing of the door in the animal facility results in a brief decrease in locomotor activity (personal observations). This may explain the decrease in break-dancing after the tone was played since the mole-rats usually froze upon hearing it.

In terms of latency, the type of stimulus did not have a significant effect on the onset of the break-dancing behavior after the onset of the stimulus. The control for odor (water) was not included in statistical tests because the average latency of the expression of the behavior was beyond 2 minutes, meaning that break-dancing occurred after the water on Wattman paper was no longer in the cage. Thus, it is likely that the mole-rats were break-dancing in response to something other than the control, such as the air movement caused by the lid being opened to remove the Wattman paper. The results indicate that there is no difference in motivation to respond to the various stimuli via break-dancing.

Overall, out of five stimulus test conditions, mole-rats break-dance significantly more after experiencing vibrations and air currents in breach simulations. This could mean that break-dancing is used to locate breaches in tunnels or a version of seismic signaling unique to DMR. These findings provide a framework for future research aimed at identifying the function of this behavior.

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Chapter 4: Conclusion

In our observational study, we determined that the break-dancing behavior is expressed at all ages and in both male and female DMR. However, breeders almost never exhibited the behavior compared to their non-reproductive offspring. These findings indicate that there is a social status component to the behavior, further differentiating the two castes. These findings are consistent with breeder's main role in the colony, which is to produce offspring, rather than foraging or maintenance of the tunnel system. Further, our experiment suggests this behavior serves multiple purposes related to breach detection and tunnel maintenance as well as seismic communication. Lastly, the results indicated that the behavior is not a result of general arousal to all environmental stimuli.