Alone, in the dark: The extraordinary neuroethology of the solitary blind mole rat

Yael Kashash[1], Grace Smarsh[1,2], Noga Zilkha[1], Yossi Yovel[2], Tali Kimchi[1]*

[1]Department of Brain Sciences, Weizmann Institute of Science, Rehovot, Israel; [2]School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel

Abstract: On the social scale, the blind mole rat (BMR; *Spalax ehrenbergi*) is an extreme. It is exceedingly solitary, territorial, and aggressive. BMRs reside underground, in self-excavated tunnels that they rarely leave. They possess specialized sensory systems for social communication and navigation, which allow them to cope with the harsh environmental conditions underground. This review aims to present the blind mole rat as an ideal, novel neuroethological model for studying aggressive and solitary behaviors. We discuss the BMR's unique behavioral phenotype, particularly in the context of 'anti-social' behaviors, and review the available literature regarding its specialized sensory adaptations to the social and physical habitat. To date, the neurobiology of the blind mole rat remains mostly unknown and holds a promising avenue for scientific discovery. Unraveling the neural basis of the BMR's behavior, in comparison to that of social rodents, can shed important light on the underlying mechanisms of psychiatric disorders in humans, in which similar behaviors are displayed.

Introduction

In the animal kingdom, social behavior strategies vary substantially within and between species, from a completely solitary lifestyle, to a eusocial way of life (reviewed by [*Zilkha et al., 2021*]). In social mammalian species, social structures of dyads, families or larger groups of various sizes are common (*Prox and Farine, 2020*), and social isolation is experienced as a potent stressor, which often leads to debilitating psychological, behavioral, and physiological effects (*Mumtaz et al., 2018*; *Leigh-Hunt et al., 2017*). In humans for example, prolonged social isolation due to the COVID-19 pandemic, was reported to have led to increases in cardiovascular disease cases, and cognitive deteriorations like depression and anxiety, in the worldwide population (*Pietrabissa and Simpson, 2020*; *Taheri Zadeh et al., 2021*). Social isolation in prairie voles was shown to produce cardiovascular dysfunctions and depression (*McNeal et al., 2014*), and socially isolated male mice showed impaired GABAergic function and increased aggressiveness (*Matsumoto et al., 2005*). In some species, however, social isolation is not experienced as a stressor, as they have evolved for solely solitary living. Within these species are large land predators such as the Eurasian lynx (*Lynx lynx*) (*Breitenmoser-Würsten et al., 2007*), and small rodents such as Heermann's kangaroo rats (*Dipodomys heermanni*) (*Yoerg, 1999*). Interestingly, out of 19 known subterranean rodent genera, 14 are solitary (*Nevo, 1979*). Even more remarkable is that within this subterranean niche, mole rats range across the entire spectrum of sociality. For example, the naked mole-rat (NMR; *Heterocephalus glaber*) and Damaraland mole-rat (*Fukomys damarensis*) are eusocial, residing in large underground communal colonies, and are in fact the only two known eusocial species within the Mammalia class (*Bennett and Jarvis, 1988*; *Barker et al., 2021a*; *Figure 1*). Highveld mole-rats (*Cryptomys hottentotus*) are social, living in small, transient familial groups (*Bennett and Faulkes, 2000*; *Moolman et al., 2006*; *Figure 1*), and Cape mole-rats (*Georychus capensis*) live alone in solitary burrows (*Du Toit et al., 1985*; *Figure 1*). This variation of social strategies amongst subterranean rodent species provides a unique opportunity for comparative
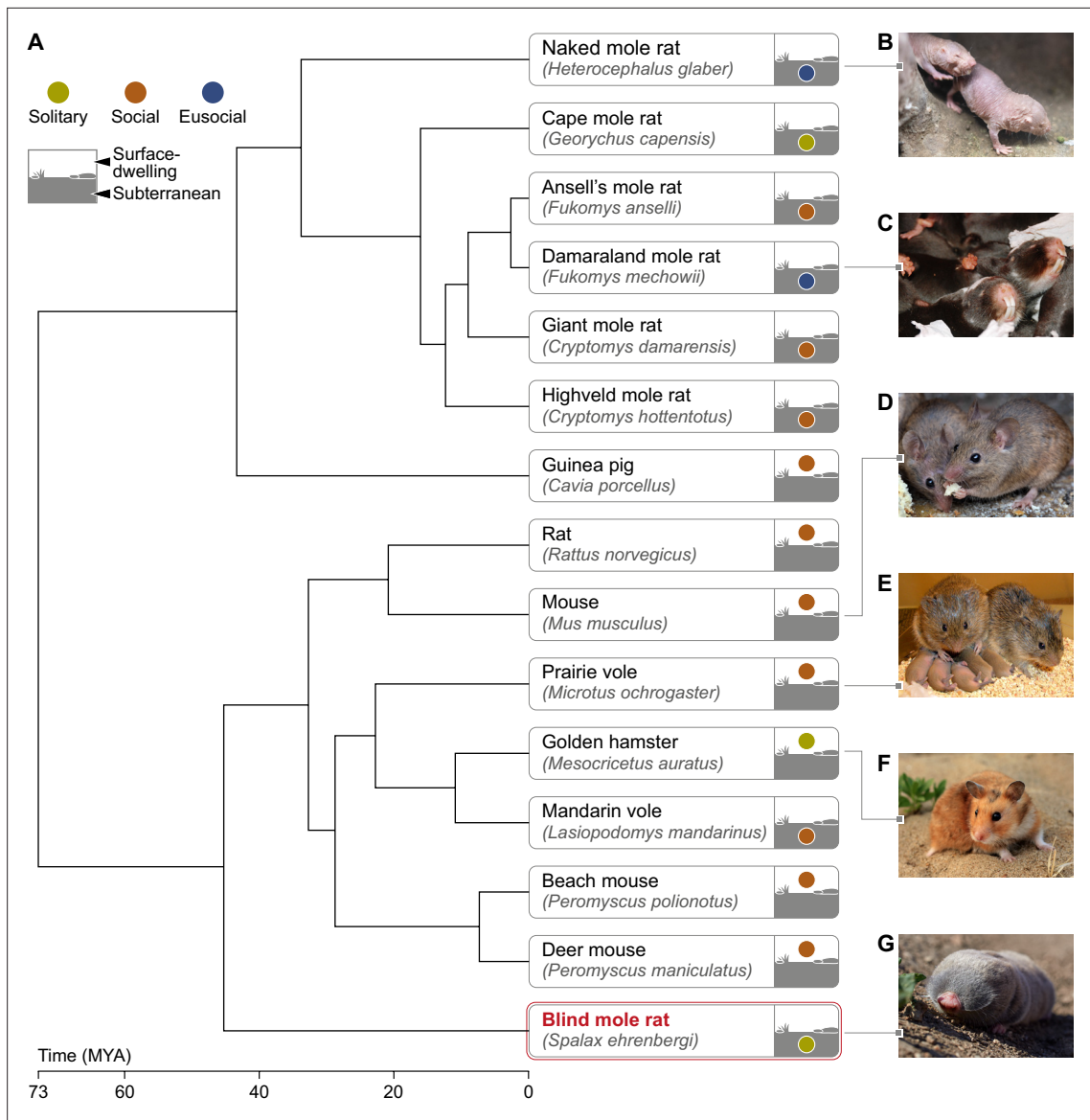
Figure 1. Phylogeny of mole rats and relatives subterranean and surface-dwelling rodents. (**A**) Phylogenetic tree generated by TimeTree software (http://www.timetree.org) displaying the evolutionary divergence of the BMR in relation to primary rodent species mentioned in this review. (**B**) Naked mole rat (*Heterocephalus glaber*) (**C**) Damaraland mole rat (*Fukomys damarensis*) (picture courtesy of Dr. Markus Zöttl) (**D**) Mouse (*Mus musculus*) (**E**) Prairie vole (*Microtus ochrogaster*) (picture courtesy of Prof. Larry Young) (**F**) Golden hamster (*Mesocricetus auratus*) (**G**) Blind mole rat (*Spalax ehrenbergi*). Time of divergence is indicated on the time scale, in millions of years ago (MYA). The color of the circle in the icon of each rodent indicates the sociality level (solitary/social/eusocial) of the species. The location of the circle distinguishes surface-dwelling from subterranean rodents. Subterranean rodents were defined as such, if they spend most of their lives in sealed underground burrows (*Nevo, 1999*).

studies to investigate the neural and evolutionary substrates driving the transitions across the 'social scale' (*Kimchi and Terkel, 2002*; *Nevo, 1999*).

On this vast range of sociality among subterranean rodents, the blind mole rat (BMR), of the *Spalax ehrenbergi* superspecies (Family: Spalacidae), represents an extreme. It is an exceedingly solitary and territorial subterranean rodent that lives entirely within self-excavated underground tunnel systems. The BMR, weighing 100–250 g (*Lacey et al., 2001*), can be found across a variety of habitats in the middle east (*Nevo, 1961*; *Nevo, 1985*). Thus far, BMRs have taken the interest of scientists mostly due to their physiological adaptations to the hypoxic underground habitat, high longevity of 20 years or more, and cancer resistance (*Manov et al., 2013*; *Schmidt et al., 2017*; *Shams et al., 2005*). Here, we propose the BMR as a model for deciphering the mechanisms underlying anti-social, solitary

behaviors, and for studying extreme aggressiveness manifested by individuals of both sexes. This model might be a crucial piece in the 'neural basis of social behavior' puzzle. Mice (*Mus musculus*) and rats (*Rattus norvegicus*), the most commonly used animal models in neuroscience (*Ellenbroek and Youn, 2016*), are considered highly social animals, and thus are not suitable for answering many scientific questions regarding the mechanisms controlling naturally-occurring anti-social and solitary behaviors. In recent years, there is a growing consensus among neuroscientists about the need for diversification of animal models (*Brenowitz and Zakon, 2015*; *Hale, 2019*; *Remage-Healey et al., 2017*; *Yartsev, 2017*). We suggest that the blind mole rat makes an ideal model organism for unraveling many neuroethological questions, such as: what is it in the BMR's brain that makes it so aggressive and territorial? Why are social stimuli considered stressors for this animal? What are the sensory signals, circuits and neuromodulators controlling these behaviors? Are there evolutionary conserved mechanisms controlling anti-social behaviors across mammalian species? In addition, uncovering the brain mechanisms underlying the BMR's sensory adaptations, its exceptionally solitary lifestyle and its extreme conspecific aggression, can serve as a prolific path for studies of brain functions associated
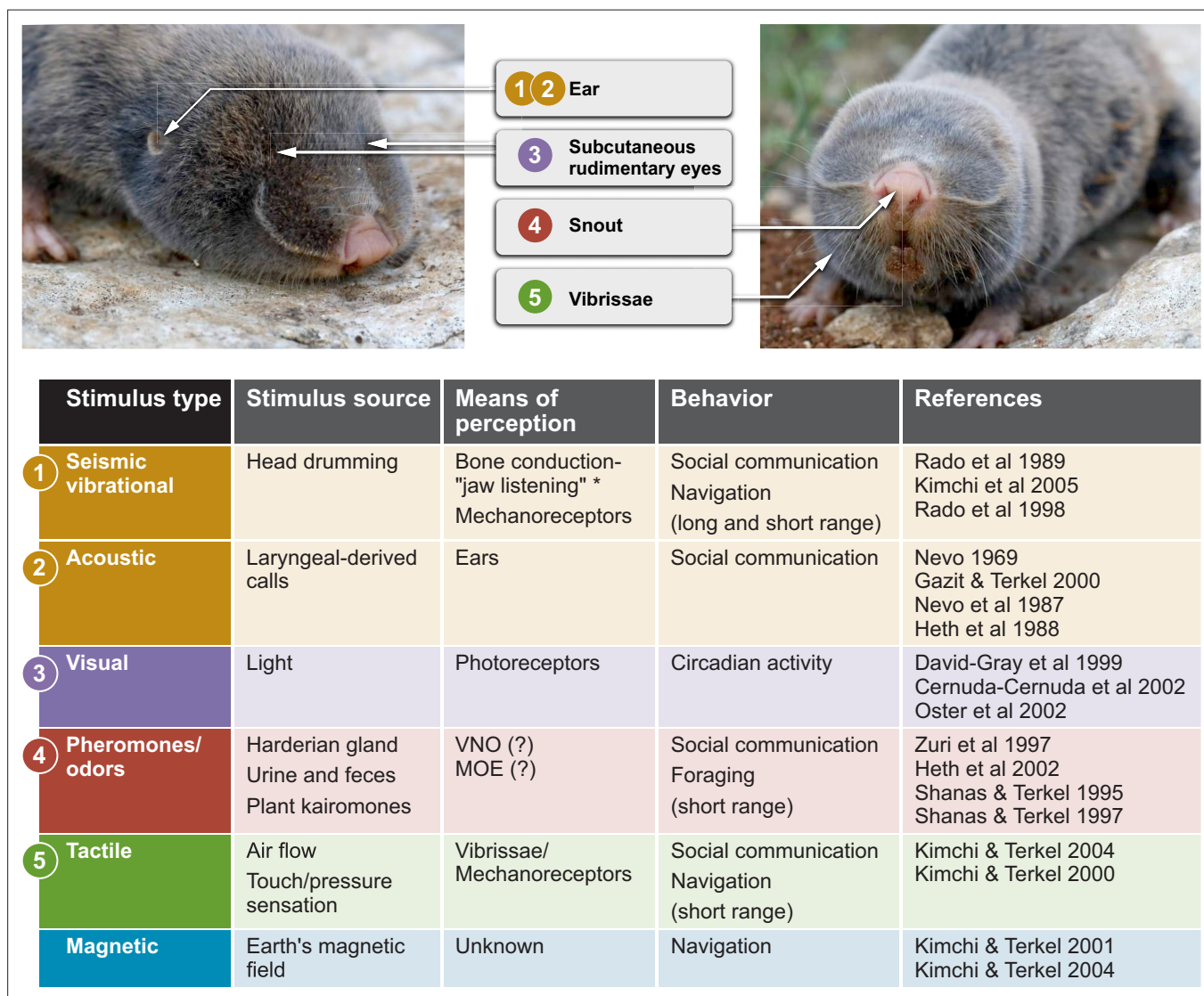

Stimulus type	Stimulus source	Means of perception	Behavior	References
1 Seismic vibrational	Head drumming	Bone conduction- "jaw listening" * Mechanoreceptors	Social communication Navigation (long and short range)	Rado et al 1989 Kimchi et al 2005 Rado et al 1998
2 Acoustic	Laryngeal-derived calls	Ears	Social communication	Nevo 1969 Gazit & Terkel 2000 Nevo et al 1987 Heth et al 1988
3 Visual	Light	Photoreceptors	Circadian activity	David-Gray et al 1999 Cernuda-Cernuda et al 2002 Oster et al 2002
4 Pheromones/ odors	Harderian gland Urine and feces Plant kairomones	VNO (?) MOE (?)	Social communication Foraging (short range)	Zuri et al 1997 Heth et al 2002 Shanas & Terkel 1995 Shanas & Terkel 1997
5 Tactile	Air flow Touch/pressure sensation	Vibrissae/ Mechanoreceptors	Social communication Navigation (short range)	Kimchi & Terkel 2004 Kimchi & Terkel 2000
Magnetic	Earth's magnetic field	Unknown	Navigation	Kimchi & Terkel 2001 Kimchi & Terkel 2004

Figure 2. Sensory perception and unique adaptations in the blind mole rat. External morphology of the blind mole rat from a side (left) and front (right) view. Arrows point to key adaptive morphological features for sensory perception. Numbers indicate the corresponding sensory modality in the table below. The stimulus type, stimulus source, means of perception and type(s) of behavior are summarized. *Vibrational signals are perceived through the lower jaw and transmitted to the inner ear by means of bone conduction. Abbreviations: VNO, vomoronasal organ; MOE, main olfactory epithelium. Photo credit: Aviad Bar.
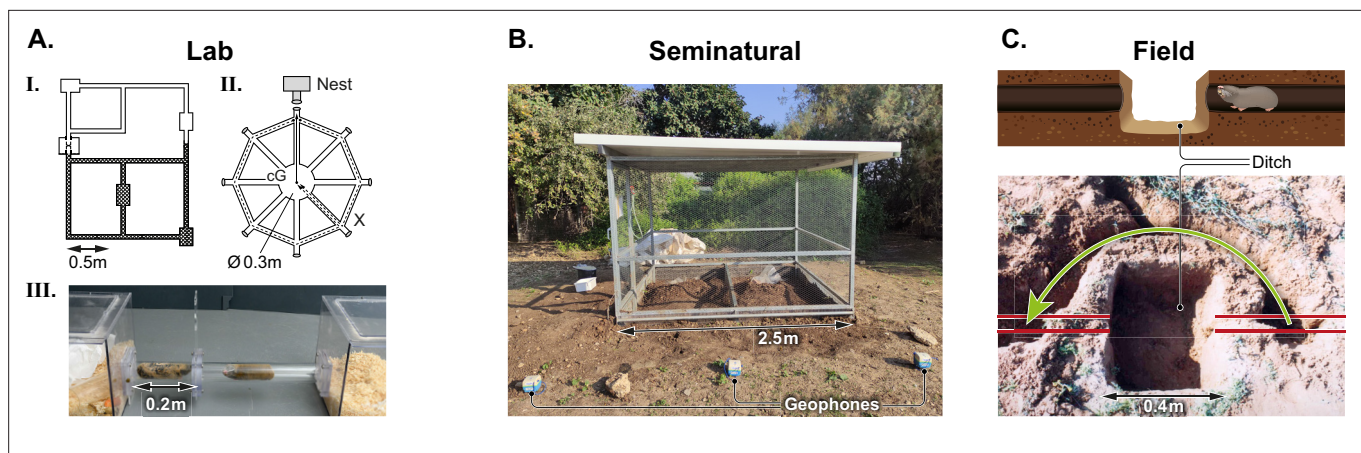
Figure 3. Experimental setups for the behavioral research of blind mole rats. (**A**) Laboratory experiments: I. Schematic representation of an experimental tunnel system made of Perspex tubes, used for the first successful breeding of BMRs in the lab. Tubes were arranged to simulate two territories with a connecting, dirt-filled nest box for mating. II. A wheel-shaped maze used for a navigation study of BMRs, consisting of eight tubes (routes) radiating from a central circle. III. An experimental setup for studying dyadic interactions between BMRs. A tube connects two Perspex home cages, with a perforated divider preventing physical contact of the two animals. (**B**) A seminatural setup: a metal mesh cage fully enclosed underground, with a central metal mesh divider allowing naturalistic experiments of two individuals simultaneously. (**C**) Field experiments: Schematic representation and photo of a field experiment demonstrating a bypass tunnel (green arrow) dug by a wild blind mole rat, following seismic 'echolocating' detection of a barrier. The barrier comprised of a ditch created by the researchers, marked in the illustration, which blocked the original tunnel (red lines).

with similar behaviors in humans. BMRs can serve as a model for understanding the neural circuits and mechanisms underlying congenital anti-social and aggressive behaviors. This may provide new knowledge on the neural basis of socially related psychiatric disorders in humans. For instance, people diagnosed on the autism spectrum, those who suffer from antisocial personality disorders, depression or neurodegenerative diseases like Alzheimer's, often present a decrease in socialization and increased aggressiveness (*Azevedo et al., 2020*; *Dutton and Karakanta, 2013*; *Gilley et al., 1997*; *Mazurek et al., 2013*; *Swearer et al., 1988*).

In the course of this review, we explore the wealth of neuroethological opportunities in the BMR, relating to social behavior and interactions, foraging and navigation. We first describe the BMR's extremely solitary behavior, its foraging and food-caching strategies, and the transient shift in sociality it needs to make with the onset of the breeding season. We also describe the BMR's unique sensory adaptations to the underground habitat (*Figure 2*), including its remarkable demonstration of brain plasticity. The BMR's magnetoreception ability is described, as well as its visual, auditory, somatosensory and olfactory systems. Yet, many questions regarding the neuroethology of the blind mole rat remain to be answered, preferably by combining lab, semi-natural and field studies (*Figure 3*). Here, we discuss some of those open questions, by summarizing what is known to date about blind mole rats and other closely related social and solitary mole rat species from a neuroethological point of view. This, we hope, will assist in gaining further insights on the neural basis of this extraordinary animal's behavior, which we consider an excellent neuroethological model.

Behavior of the blind mole rat
Territoriality and aggression
With the exception of short mating and lactating periods during the winter (the wet season), male and female blind mole rats reside alone throughout the year, patrolling their tunnels and defending their territories from conspecifics and congenerics (*Nevo, 1961*; *Rado et al., 1993*). For the BMR,
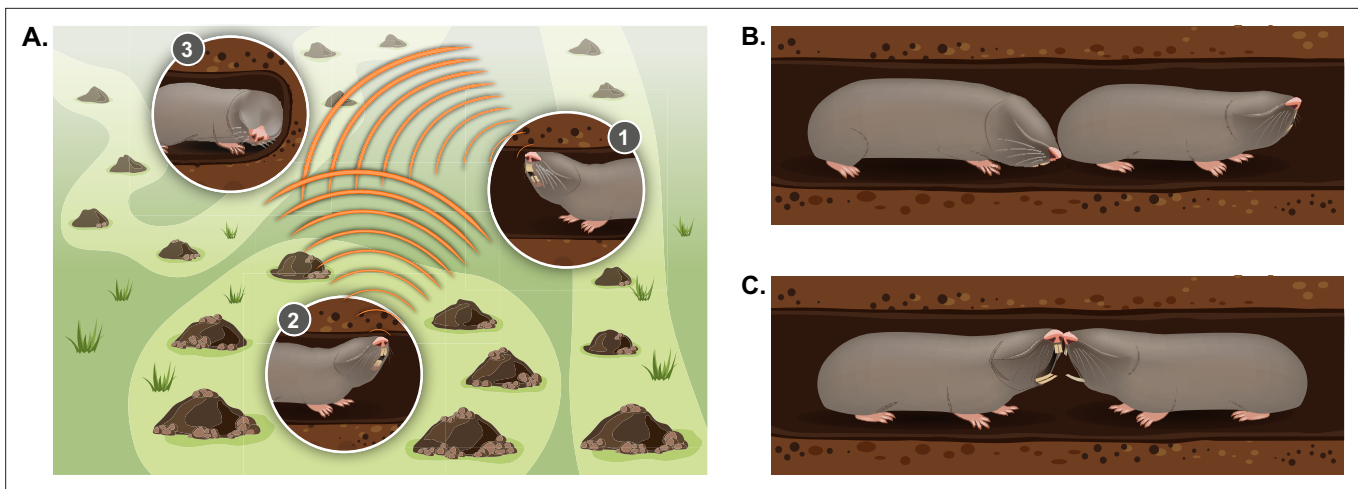
Figure 4. Typical social behaviors displayed by blind mole rats. (**A**) An illustration of the 'social communication network' between BMRs in neighboring territories using seismic signaling. BMRs #1 and #2 are head drumming back and forth on the tunnel ceiling; BMR #3 is 'jaw listening' by pressing its jaw against the tunnel wall. (**B**) Courtship behavior: a male BMR sniffing the genitals of a female BMR as part of the courtship process during the mating season. (**C**) An aggressive encounter between an intruder and a territory holder, including teeth baring and biting. Aggressive encounters typically lead to injuries and/or death of one or both rivals.

close encounters from territory encroachment are experienced as extremely stressful, and usually result in severe physiological stress and extreme aggression, frequently leading to the death of one or both individuals (*Nevo, 1961*; *Nevo, 2013*; *Zuri et al., 1998b*, *Zuri and Terkel, 1998*). Agonistic and aggressive behaviors in BMRs are manifested by 'retreat and attack' postures and by 'bulldozing' a soil plug using the snout (*Guttman et al., 1975*). Other aggressive gestures include strong strikes and opponent-pushing with the head, open mouth sniffing (exposed incisors; *Figure 4*) and biting (*Nevo et al., 1986*). These behaviors were shown to increase where there is more competition for resource availability (*Nevo et al., 1982*). Females were reported to present lower aggression intensity compared to males (*Nevo et al., 1986*) nevertheless, the behavioral component of these behaviors was shown to be independent of testosterone levels in male BMRs (*Gottreich et al., 2001*). The territorial nature, extreme seasonality of breeding, and subterranean lifestyle of blind mole rats make them an excellent model for examining decision making, sensory perception in the dark and neural substrates underlying the transition from anti-social to social behaviors during the reproductive season.

Like other territorial animals, the spatial ecology and social organization of the blind mole rat can be considered a type of social communication network. In this network, repeated communication signals detected from a distance may advertise locations of neighbors and function to maintain boundaries and conspecific spacing (*McGregor, 1997*; *Figure 4*). Thus, the BMR's specialized vibrational long-distance communication system, in the form of 'head drumming' (see section 'Vibrational communication'), creates a specialized communication network between neighbors (*Heth et al., 1987*; *Rado et al., 1987*). This network is ever-shifting and dynamic. During the active winter months, individuals have many adjustments in territory size and location (*Zuri and Terkel, 1996*), and they must decide where to tunnel and whether to avoid or engage a neighbor in order to expand their territories. These decisions are likely heavily influenced by information from the head drums and by the individual's experience. It has been noted that BMRs engage in head drumming 'duets' back and forth across territories (*Rado et al., 1987*), but the types of information encoded in the signal (for example the signaler's level of dominance, sex, age, or individual identity) are not well understood (*Randall, 2013*; *Seyfarth and Cheney, 2003*; *Tibbetts and Dale, 2007*). Furthermore, whether additional signal features are modified in heightened motivational states (for example high vs. low aggression) has not been addressed (*Bradbury and Vehrencamp, 2011*). Understanding the neural processing underlying these finer cues of vibrational signaling dynamics, and how they result in a behavioral decision, will provide the mechanistic basis of territory maintenance and social avoidance, as well as social approach (i.e. finding a potential mate).

Reproductive behavior

BMRs are seasonal breeders (*Shanas et al., 1995*), for whom the active rainy season represents a crucial time in which males decide to burrow new tunnels to navigate toward a female. The approached female, on her end, can engage in either territorial battles or mating (*Nevo, 1961*; *Nevo, 1969*). Targeting and navigating underground toward a distant female is a complex sensory challenge, which is likely facilitated initially by long-distance head drumming, along with magnetic compass orientation (*Kimchi and Terkel, 2001*) and path integration for navigation (*Kimchi et al., 2004*). At a close distance to the female's tunnel, courtship ensues, involving multimodal signaling including seismic head drums, vocal 'purrs' and olfactory cues, and engaging in tactile behaviors until the female decides to mate with the male (*Gazit and Terkel, 2000*; *Nevo, 1961*; *Nevo, 1969*; *Shanas et al., 1995*; *Figures 2 and 4*). Copulatory pairs spend brief periods together, retreating to their individual territories after mating (*Gazit and Terkel, 2000*).

A female will respond to the male's courtship gestures based on her sensory perception and prior experience, to ultimately allow a typically aggressive male to approach, and subsequently mate with (*Kavaliers and Choleris, 2017*). To date, the mate choice strategy of female blind mole rats has not been thoroughly studied. One particular study examined reactions of females to calls from males belonging to the four chromosomal species of blind mole rats in Israel (2n=52; 2n=54; 2n=58; 2n=60) (*Nevo et al., 1987*). It was observed that estrous females are able to discriminate chromosomal subspecies of male BMRs by their courtship calls, and that in most cases, estrous females would prefer the calls of their homospecific mates over those of heterospecific ones (*Nevo et al., 1987*). Furthermore, the switch from extremely avoidant behaviors to actively seeking and encountering a mate represents a drastic shift in behavior by both males and females. Another interesting shift in the BMR's behavior accrues in juveniles, which switch from socially interacting with their mother and siblings, to presenting an aggressive behavior toward them. Gestation period in BMRs is 34 days, after which the female delivers a litter of 3–4 pups on average (*Gazit et al., 1996*). Mother and pups communicate by vocalizations in the first stages of ontogeny, and gradually shift to seismic communication of head drumming duets (*Rado et al., 1991b*). Interestingly, *Gazit and Terkel, 1998* reported sex differences in mother-pup interactions prior to a complete dispersal, as mother's communication and aggression toward male pups was longer and more frequent compared to those toward female pups. The higher aggression toward male pups could be the motivating factor that drives juvenile males to disperse earlier than females, and establish more distant territories, preventing inbreeding. Overall, the transition from a social lifestyle during pup rearing, to a solitary lifestyle, is accompanied by increased aggression toward the pups, alongside increased aggression between siblings (*Gazit and Terkel, 1998*; *Zuri and Terkel, 1998*). This process leads to the gradual dispersal of the juveniles, starting approximately 2 months after parturition (*Gazit and Terkel, 1998*), and ending in the individual establishment of their own solitary territories at the age of approximately 3 months (*Rado et al., 1991b*).

The biological basis of these social lifestyle switches is unknown. Many environmental signals are known to act as timing cues, that alter the neuroendocrine substrates that regulating reproductive physiology and behavior (*Follett, 2015*). Despite residing almost exclusively underground, BMRs were shown to integrate photoperiodic changes and entrain a circadian activity rhythm by light received through their atrophied eyes (see section 'Circadian rhythm') therefore, changes in day length may be involved in the shift from solitary to mate-seeking behavior. In male prairie voles (*Microtus ochrogaster*), alteration of both temperature and photoperiod caused regression in synthesis of gonadotropin-releasing hormone, and in their reproductive function (*Kriegsfeld et al., 2001*). Thyroid hormones were also implicated in seasonality and breeding, as was demonstrated by Yoshimura and colleagues (reviewed in [*Nakane and Yoshimura, 2014*; *Yoshimura, 2013*]). Since BMRs breed in the wintertime, when ambient temperatures drop, it is possible that consequent elevated T3 levels enhance the onset of their reproductive behavior. Other environmental cues such as soil moisture content, sudden abundance of food associated with the rainy mediterranean winter, and even the composition of food resources, most probably play a role in the initiation of the breeding season. For example, in female townsend's voles (*Microtus townsendii*), the addition of a specific plant metabolite during the non-breeding season, increased serum follicle-stimulating hormone levels and the size of reproductive organs (*Schadler et al., 1988*), and also resulted in a 4-week advancement of sexual maturation and breeding (*Korn and Taitt, 1987*).

The neural mechanism underlying behavioral plasticity in the 'anti-social brain' can be addressed within the framework of the 'Social Behavior Network', the set of interconnected brain regions implicated in the control of multiple forms of social behavior (*Cummings and Ramsey, 2015*; *O'Connell and Hofmann, 2011*; *Prounis and Ophir, 2020*).

Foraging behavior

BMRs are generalists that forage and cache encountered food items, such as geophytes and herbaceous plants (*Galil, 1967*; *Heth, 1989*, *Lövy et al., 2015*). The BMR's foraging and food-caching behaviors are essential to ensure survival throughout the year (*Rado et al., 1993*; *Vleck, 1979*). When foraging in densely populated areas, BMRs must decide in which direction to tunnel based on environmental conditions such as moisture content, plant olfactory compounds and locations of nearby neighbors, from whom they must avoid (*Heth et al., 2002*; *Rado et al., 1993*; *Gazit et al., 1997*). Digging is very energetically costly. Thus, it likely benefits subterranean rodents to collect as many food types as they encounter within the habitat (*Heth, 1989*, *Heth and Todrank, 2007*, *Nevo, 1961*; *Vleck, 1979*).

In the summer, individuals stay largely inactive in tunnels at deeper and cooler depths (>40 cm) (*Rado et al., 1993*), where food is less available. Food caches support the BMR's diet during this season (*Lövy et al., 2015*). In addition to remembering the location of their food caches, food-caching animals are often faced with the task of remembering which food items are stored, and the timing of storage, as different food items expire at different rates (*Smith and Reichman, 1984*). This "what, when, where" type of memory is referred to as episodic-like memory and has been well studied in birds (*Roberts, 2006*), but was also demonstrated in rats (*Babb and Crystal, 2006*; *Yi et al., 2021*). BMRs were shown to have far superior spatial memories compared to rats, learning a maze significantly faster, and retaining 45% of their performance 120 days later (*Kimchi and Terkel, 2001*). Other mole rat species, the Damaraland and Cape mole rats, have been shown to be able to learn and retain memory of the location of food rewards within a maze (*Costanzo et al., 2009*). While it is unclear how many food caches BMRs may have branching off their tunnels, which can be as long as 100 m, it is likely that their excellent spatial memory facilitates food cache revisiting (*Lövy et al., 2015*). Such high cognitive abilities probably integrate high spatial memory with specialized sensory abilities such as magnetoreception (*Kimchi et al., 2004*; *Kimchi and Terkel, 2001*), in food caching mole rat species (*Lange et al., 2005*). The underlying mechanisms, as well as basic behaviors involved in revisiting food caches and selecting food items, in line with prior life events (for example parturition), can be examined with both lab and semi-natural setups (*Figure 3*).

Sensory adaptations to a subterranean, solitary lifestyle

Visual system

The BMR's eye

While blind mole rats appear as if they have no eyes, they do possess rudimentary eyes (less than 1 mm in diameter), that are covered by furred skin (*Cooper et al., 1993b*, *Haim et al., 1983*; ; *Rado et al., 1992*; *Figure 2*). The lens of the BMR is degenerated and embedded within a hypertrophied harderian gland (*Cooper et al., 1993b*, *Haim et al., 1983*; *Rado et al., 1992*). The BMR's retina contains < 900 ganglion cells (*Cooper et al., 1993a*), a significantly low number compared to >50,000 cells found in rats, for example (*Gao et al., 2016*). Moreover, brain structures involved in image processing are severely regressed and dysfunctional in the BMR (*Cooper et al., 1993a*). Multiple studies demonstrate that the non-functional visual centers in the BMR's brain have been replaced by the auditory modality. For instance, the dorsal lateral geniculate body, which is the primary visual nuclei in the thalamus of sighted mammals, that sends visual information to the visual cortex, was reported to be strongly activated by auditory stimuli in BMRs (*Bronchti et al., 2002*; *Bronchti et al., 1989*; *Heil et al., 1991*). Although the BMR's retina lacks short-wave opsine cones (*David-Gray et al., 2002*), it includes at least three types of photoreceptors (rodopsin, coneopsin and L/M cone opsin) that collect the scant light penetrating the soil (*Burda, 2006*; *David-Gray et al., 1999*; *Esquiva et al., 2016*). Overall, the BMR's eye can be considered as a light-meter corresponding to the 'non-image forming' system found in the eye of sighed mammals.

Circadian rhythm

In mammals, light perceived through the retina uses the common photoreceptors (i.e. rods and cones) for image formation, and the photoreceptor melanopsin for the non-image forming system. Melanopsin is the driving force for the circadian timing system, that initiates the animal's physiology and behavior in distinct times and periods (*Freedman et al., 1999*; *Hannibal, 2021*). The BMR's eyes respond to light stimulation and provide information used to entrain circadian and annual cycles generated by the suprachiasmatic nucleus (SCN), through the neuronal pathway of the retinohypothalamic tract (*Cernuda-Cernuda et al., 2002*; *David-Gray et al., 1999*; *Hannibal, 2002*; *Moore et al., 1995*; *Oster et al., 2002*). Therefore, despite being blind, light induces gene expression in the SCN (*Vuillez et al., 1994*) and entrains circadian rhythms of locomotor behavior in the BMR (*David-Gray et al., 1998*; *Rado et al., 1991a*). These reactions to light rely upon retinal photoreceptors, since enucleation abolished them (*David-Gray et al., 1998*; *Pevet et al., 1984*; *Rado et al., 1991a*). In addition to the atrophied eyes, the BMR's harderian gland is also involved in photoperiodic perception, as it is able to synthesize melatonin (*Balemans et al., 1980*), and it was shown to be involved in photoperiodic detection (*Pevet et al., 1984*). Melatonin receptors were also found in the BMR's harderian gland, and were suggested to take part in a negative feedback control of melatonin production (*Gilad et al., 1997*). Interestingly, the eusocial, subterranean Damaraland mole-rat was also shown to possess a circadian melatonin rhythm that is modulated according to photoperiodic changes (*Richter et al., 2006*).

Insights on light perception in the BMR emphasize its relevance as a model for studying re-routing of sensory modalities into processing areas of other sensory modalities, after evolution has neutralized its original output. Such cross-modality reorganizations in animal models are often induced artificially (for example by sensory deprivation or neuronal manipulation). However, the visual system of the blind mole rat is naturally and congenitally adapted to life in the dark, rendering it a very attractive subject for studying evolutionary plasticity in the central nervous system (CNS) and for revealing the mechanism of neuronal compensation.

Magnetoreception

Magnetoreception, the ability to perceive the earth's magnetic field, is a sensory modality observed in various vertebrate species (*Begall et al., 2014*), some invertebrates taxa (*Hsu and Li, 1994*; *Lee et al., 2021*) and even in plants (*Galland and Pazur, 2005*). Unlike surface-dwelling rodents, subterranean rodents lack some external stimuli that are normally used for spatial orientation, such as stars, sun light azimuth, and other visual cues. *Kimchi and Terkel, 2001* demonstrated that blind mole rats have magnetoreception abilities, and that they rely on them when choosing the locations for their nests and food caches. When shifting the polarity of the earth's magnetic field by 180°, BMRs shifted the location of their preferred nest and food cache sites accordingly (*Kimchi and Terkel, 2001*). To this day, there is a debate regarding the magnetosensory organ of terrestrial animals, and there is evidence for both light-dependent and light-independent mechanisms of magnetoreception. Are magnetoreceptors located in the minute eyes of mole rats, or are they located elsewhere? In birds and other vertebrates, the ability to use the earth's magnetic field for spatial orientation was shown to be light dependent, apparently perceived through eye receptors (*Phillips and Borland, 1992*; *Wiltschko et al., 2008*; *Wiltschko et al., 1993*; *Wiltschko and Wiltschko, 1982*). In addition, following surgical removal of their eyes, individual Ansell's mole-rat (*Fukomys anselli*) demonstrated impaired magnetic sensing, supporting the hypothesis that in mole rats, magnetoreception receptors are located in the cornea (*Caspar et al., 2020*). However, some observations in BMRs suggest that the their magnetoreception is independent of light, as experiments were conducted in total darkness (*Kimchi and Terkel, 2001*). This finding is supported by a study of another mole rat species, the Zambian mole rat (*Fukomys amatus*), that was shown to be independent of light in its perception of the earth's magnetic field (*Marhold et al., 1997*). Further research based on magnetic compass orientation in mole rats, and in particular the blind mole rat, is needed, as is further research investigating the location of relevant magnetoreceptors and sensory pathways.

Auditory system

Hearing sensitivity

For any animal that is active where and when visual cues are scarce, acoustic vocalizations usually become an important sensory modality for navigation (for example echolocation), or for detection and communication with conspecifics (*Bradbury and Vehrencamp, 2011*). However, for subterranean mammals including blind mole rats, the underground environment creates very specific acoustic conditions. Tunnels create large surface areas at close proximity to the emitter of the signal, causing high levels of attenuation of high frequencies sounds through absorption, and simultaneously amplification of noise from reverberation (*Begall et al., 2007*). Accordingly, fossorial and subterranean animals generally hear better at low frequencies and have restricted hearing ranges, compared to surface-dwelling rodents that have been known to produce frequencies as high as in the ultrasonic range (*Dent et al., 2018*; *He et al., 2021*). The Highveld mole rat (*Müller and Burda, 1989*) and the Zambian mole rat (*Brückmann and Burda, 1997*), both subterranean rodents, are more sensitive to very low frequencies (0.8 kHz) while the surface-dwelling feral house mouse (*Heffner and Masterton, 1980*) is most sensitive to higher frequencies (16 kHz).

In addition, peak sensitivities for hearing vary substantially among rodents (*Gerhardt et al., 2017*; *Heffner and Heffner, 1990*; *Heffner and Heffner, 1992*; *Heffner and Heffner, 1993*). For example, peak sensitivity in the surface-dwelling guinea pig (*Cavia porcellus*) is –9 dB SPL (sound pressure level) (*Prosen et al., 1978*), while in the subterranean naked mole rat it is just 35 dB SPL (*Heffner and Heffner, 1993*). Results from behavioral audiograms showed that trained blind mole rats can hear between 54 Hz and 5.6 kHz at an amplitude of 60 dB SPL , with peak sensitivity at 1 kHz at 32 dB SPL (*Heffner and Heffner, 1992*). Additionally, blind mole rats have poor sound localization abilities, as demonstrated from playback of left and right speakers with 180° of separation (*Heffner and Heffner, 1992*). Blind mole rats cannot localize signals less than 400 ms in duration, and performed best at localizing sound bursts of 1.2ms (*Heffner and Heffner, 1992*). The lower hearing sensitivity and minimal localization ability are apparent in the morphology of the BMR, which lacks an external pinna of the outer ear (see ear opening location in *Figure 2*). The BMR's middle and inner ear are uniquely structured, creating inefficient transmission of airborne sound (*Rado et al., 1989*).

Vocalizations

The low-frequency repertoires of different mole rats vary across species, consisting of a variety of social calls (*Knotková et al., 2009*). Giant mole rats (*Fukomys mechowii*) were demonstrated to have a repertoire of 14 call types as determined by behavioral context, such as teeth-fencing and predator alarm, and by spectro-temporal features (*Bednářová et al., 2013*). In accordance with their low frequency hearing ranges, these calls are low in frequency, with peak frequencies of less than 5 kHz (*Bednářová et al., 2013*). The eusocial naked mole rat was recently shown to have dialects in the 'soft chirp' call type across colonies that signifies group membership (*Barker et al., 2021b*). Since BMRs are spatially isolated it is unlikely that their social calls can be transmitted or detected across territories through the thick soil substrate (*Heth et al., 1986*; *Narins et al., 1992*).

The full vocal repertoire of the BMR has not yet been described. At least six call types determined by behavioral context, all with frequencies below 8 kHz, have been noted thus far (*Capranica et al., 1974*). Different call types are used to facilitate mother and pup communication (*Capranica et al., 1974*; *Gazit and Terkel, 1998*; *Rado et al., 1991b*), and used in male courtship displays during the mating season (*Gazit and Terkel, 2000*; *Nevo, 1969*). These courtship calls differ in frequency and temporal components across the *Spalax* chromosomal subspecies, and appear to play a role in assortative mating between the neighboring populations (*Heth et al., 1988*; *Nevo et al., 1987*) (see section 'Reproductive behavior'). Distress calls with peak frequencies between 4 and 6 kHz have also been opportunistically observed in lab studies (*Bronchti et al., 1989*). However, variation in spectro-temporal features by individuals and by level of stress, as well as variation in use in the context of multimodal signaling (for example head drums and physical encounters) have not been studied.

Vibrational communication

The auditory system of the BMR is uniquely adapted to detect and process non-vocal vibrational (seismic) signals (*Figure 4*). The use of substrate-borne vibrational signals in animals is not well understood, but has been observed in elephants, arthropods such as spiders, some reptiles, and a number

of fossorial or semi-fossorial rodents, including kangaroo rats (Heteromyidae), African mole rats (Bathyergidae), and blind mole rats (Spalacidae) (*Hill, 2001*; *Narins et al., 2009*). The mechanism for production of vibrational signals varies across taxa and species. These signals are used for communication between conspecifics, for mating and/or inter-individual spacing (for example territory maintenance), targeting prey and even for detecting obstacles (*Hrouzková et al., 2018*; *Kimchi et al., 2005*; *Narins et al., 2009*; *Narins et al., 1997*; *Randall and Lewis, 1997*).

A BMR produces vibrational signals by drumming on the ceiling of its tunnel with the large, flattened portion of its head, producing bursts of head drums (approx. 2–4 drums per burst, 0.3 s duration) (*Heth et al., 1987*; *Rado et al., 1987*; *Figure 4*). Seismic signals range in the frequency of approximately 100–250 Hz and may travel as far as 10 m or more (*Heth et al., 1987*; *Rado et al., 1987*). Perception of seismic signals is achieved in two ways, one by pressing the side of their lower jaw against the tunnel wall, which transmits the signals to the inner ear by means of bone conduction (*Mason et al., 2010*; *Rado et al., 1989*; *Figure 4A*). The Second is via mechanoreceptors located on their paws (*Kimchi et al., 2005*). "Jaw listening" behavior was observed in laboratory conditions in which BMRs in Perspex tubes alternated between head drumming and placing their jaws on the tube wall (*Heth et al., 1987*; *Rado et al., 1987*). In field experiments, while radio-tracking BMRs using very high frequency telemetry, Zuri & Terkel observed that individuals patrolled their territories with regular pauses for 5–120 sec, suggesting that they stop to 'listen' for seismic activity of neighbors (*Zuri and Terkel, 1998*). In addition, in a lab study using a maze, individuals paused at maze junctions and placed their jaws against the tube (*Kimchi and Terkel, 2004*). Providing a vibration stimulus in contact with the lower jaw evoked responses in the auditory brainstem, and bilaterally deafened mole rats, showed loss of response and eventual ceasing of head drumming behavior in the course of 4–6 weeks (*Rado et al., 1998*). Furthermore, the occipital cortex, usually associated with vision, was shown to be activated by frequencies corresponding to both vibrational and acoustic signals (*Bronchti et al., 2002*; *Heil et al., 1991*; *Sadka and Wollberg, 2004*). In one study, cortical activation was demonstrated via playbacks of acoustic stimuli including clicks, noise, and tones while collecting extracellular single unit recordings in the cortex (*Sadka and Wollberg, 2004*). Specifically, two clusters of cells fired in response to frequencies centered around 2.5–4.4 kHz, matching airborne social vocalizations, and to 100 Hz, matching the frequency of long-distance vibratory signals (*Sadka and Wollberg, 2004*). Further experiments using vibrational stimuli and neural recordings or MRI may confirm the convergence of vibration and auditory stimuli processing in the BMR cortex.

The general understanding of the behavioral discrimination and sensitivity of perception of vibrational waves in the subterranean environment is greatly lacking (*Hill, 2009*; *Mortimer, 2017*). The sensory sensitivity to fine signal differences and its encoding in the cortex would be a great advancement in understanding of the seismic sensory system of the BMR.

Somatosensory system

In addition to the auditory cortex, it was further shown that the BMR's somatosensory cortex also extends far into the occipital cortex (*Necker et al., 1992*; *Rehkämper et al., 1994*). This finding is a clear example of the evolutionary plasticity of the BMR's brain. The somatosensory system in the isocortex of the blind mole rat was shown to be 1.7 times larger compared to the laboratory rat, when taking into consideration the differences in body weight and brain size of the two species (*Mann et al., 1997*). Subterranean rodents, including BMRs, have a highly developed tactile sense, used as a mechanism of navigation in their complex tunnel system, and as a mechanism for detecting substrate-borne vibrational signals (*Necker et al., 1992*; *Nevo et al., 1991*; *Rehkämper et al., 1994*). They possess sensory vibrissal hairs connected to sensitive mechanoreceptors dispersed over different body parts, contributing to efficient orientation and likely path integration in their narrow burrows (*Bennett and Faulkes, 2000*; *Figure 2*). Klauer and colleagues found that the dermal papillae of the rhinarium in the BMR contains a few Merkel cell-axon complexes and simple Meissner's corpuscles. This might indicate the sensitivity of the rhinarium to vibrations and its involvement in perception of seismic signals in terms of rhythm, amplitude and frequency (*Klauer et al., 1997*). Nevertheless, it is worth noting that similar receptors were also found in the noses of rats (*Silverman et al., 1986*), a rodent species that is not known to use seismic communication. During maze learning and exploration tasks, BMRs consistently engage in a 'wall seeking' behavior, in which they press their bodies against the side of the wall, sometimes alternating sides, and brushing the vibrissae against the maze surfaces

(*Kimchi et al., 2004*). When comparing maze learning and performance, blind mole rats performed significantly better in a narrow maze which allowed constant contact with the wall, compared to a maze twice the width of their body diameter (*Kimchi and Terkel, 2000*). In contrast, rats performed better in the wider maze (*Kimchi et al., 2004*). In nature, BMRs dig their tunnels to exactly the diameter of their own body width, in order to obtain maximal tactile information (*Kimchi and Terkel, 2002*). The vibrissae hairs may provide crucial information that assists the blind mole rats to rapidly orient and move through their tunnel. This further implies that sensory acquisition from hairs that are touching tunnel surfaces or receiving fine air movements is rapidly processed by somatosensory and motor circuitries. Additionally, for naked mole rats which use their teeth for digging, foraging, social encounters, and moving pups, the incisors are represented in approximately 31% of the somatosensory cortex (*Catania and Remple, 2002*; *Park et al., 2007*). We may expect to find similarly high representation of teeth in the BMR, which are also reliant on teeth for digging, foraging, and aggressive encounters.

In mammals, oscillating signals passed to the animal by direct contact with a solid substrate can be perceived by both auditory and somatosensory mechanisms. The role of the auditory system in detection of seismic signals was discussed earlier (in the 'Vibrational communication' section). Blind mole rats have been suggested to detect vibrational signals through the somatosensory system in addition to the auditory system. Kimchi and colleagues demonstrated that BMRs use seismic signaling as an echolocation behavior (*Kimchi et al., 2005*). In field experiments, blind mole rats were able to detect obstacles placed by the researchers in their tunnels (various size ditches), and repeatedly dug around or over them. The bypass strategy varied depending on the size of the obstacle (large/small ditches), likely to minimize energetic costs (*Kimchi and Terkel, 2003a*, *Kimchi and Terkel, 2003b*; *Figure 3C*). The BMRs in these controlled field experiments were hypothesized to head drum and detect the signals reflected from the substrate barrier (air), sensing the location and size of the barrier. Unlike head drums used for intraspecific communication, these drums were higher in frequency (250–300 Hz) and produced as a single hit rather than bursts at intervals of approximately 8 s (*Kimchi et al., 2005*). Through modeling, it was demonstrated that the amplitude and frequency of the wavelengths recorded by geophones are sufficient for rapid detection of reflected waves when the individual is 30–50 cm away from an obstacle (*Kimchi et al., 2005*). However, because the reflected waves were estimated to return to the individual faster than the individual could place its jaw against the tunnel (for 'jaw listening'), the research team suspected an alternative form of vibration detection. Experimentally, it was shown that BMRs can detect seismic signals produced by a mechanical shaker or a stimulus mole rat, also via their paws (*Kimchi et al., 2005*). The glabrous (hairless) skin of the front and hind feet of the BMR contains 15–20 lamellated Pacinian corpuscles, a type of mechanoreceptor known to be sensitive to high-frequency vibrations from 10 to 400 Hz in mammals (*Kimchi et al., 2005*; *McIntyre, 1980*). Currently, these corpuscles are the only proposed receptors for somatosensory seismic sensitivity used in echolocation in BMRs. These findings open a promising research avenue, examining the role of the somatosensory cortex in encoding seismic signals for orientation skills. We may expect a pattern of frequency, amplitude and temporal entrainment of cortical neurons for object discrimination (*Prsa et al., 2021*; *Prsa et al., 2019*). It is most likely that both the auditory and the somatosensory systems are involved in vibration processing, as is the case in humans and other animal species (*Budinger et al., 2006*; *Campi et al., 2010*; *Roy et al., 2017*).

Olfaction

Olfaction, the sense of smell, plays an important role in detection of food, identification of conspecific territories and recognition of mates. For an animal as aggressive and territorial as the blind mole rat, which is also visually blind, the ability to identify odors from the surroundings is highly important in order to avoid intraspecific aggressive encounters. BMRs possess dorsoventrally flattened, wide, snouts (~15 mm wide in adults; personal observations) (*Figure 2*), that assist them in pushing out the excavated soil while burrowing, using bulldozing movements of their heads, consequently creating multiple mounds above the ground (*Figure 4*). BMRs have been shown to use olfaction to discriminate poisonous versus edible food items from the plant growth hormones, kairomones located within soil where plants had been growing (*Heth et al., 1992*, *Heth et al., 2002*).

The mammalian main olfactory system detects mainly environmental odorants (*Sanchez-Andrade and Kendrick, 2009*), while the vomeronasal organ (VNO) located at the base of the

nasal cavity, mainly detects intraspecific pheromones (*Keverne, 1999*). In mammals, particularly rodents, the VNO plays a major role in mediating socio-sexual behaviors (*Cross et al., 2020*, *Halpern and Martínez-Marcos, 2003*; *Kelliher, 2007*). As in rats (*Addison and Rademaker, 1927*), the VNO of the blind mole rat opens directly to the nasal cavity by a narrow canal, and is not connected to the oral cavity (*Zuri et al., 1998a*). In developing mole rats from infancy to adulthood, there is an approximately 8.5-fold increase in VNO length (from 1.5 mm at 4 days to 13 mm in adults) (*Zuri et al., 1998a*). This increase is much more substantial when compared to findings in African mole rat species (family *Bathyergidae*), which show postnatal vomeronasal epithelium (VNE) length increase of less than one-fold (*Dennis et al., 2020*). Moreover, in the naked mole rat, no postnatal volumetric growth was found in the VNE (*Smith et al., 2007*). This data might suggest that blind mole rats possess higher abilities for pheromone detection, in comparison to other mole rat species.

Most terrestrial vertebrates carry two large families of vomeronasal pheromone receptors: vomeronasal receptors type 1 (V1Rs) and type 2 (V2Rs) (*Nei et al., 2008*). While V1Rs are mainly involved in detecting air-borne molecules scattered in the air, V2Rs are commonly responsible for binding to water-soluble peptides abundant in aquatic environments (*Shi and Zhang, 2007*). Recently, it was shown that there has been a convergent reduction of V1Rs in different subterranean rodents, including the BMR (*Jiao et al., 2019*; *Zhao, 2021*), suggesting that pheromonal olfaction mediated by V1Rs might be reduced, as it may not be as useful as seismic communication in the underground tunnel environment.

Pheromonal signaling in the blind mole rat is used in short-distance social communication (*Figure 4C*). In the BMR's underground tunnels, there is very restricted airflow, limiting the detection distance of the signal. The BMR secretes pheromones from the large harderian gland located at the ocular orbit by self-grooming (*Shanas and Terkel, 1995*). The harderian gland is sexually dimorphic in lipid and volatile composition, and in size and weight (larger in males) (*Shanas and Terkel, 1999*). Gland size and weight also correlate with total body mass and season of the year (*Shanas and Terkel, 1999*). Secretion of pheromones by grooming during social interactions is thought to signal submissiveness and appeasement (*Shanas and Terkel, 1997*).

Urine and feces are other prominent sources for odor stimuli used by many mammalian species in a variety of behaviors (*Bronson, 1979*; *Doty, 1986*; *Macdonald et al., 1990*). Male BMRs use urine and feces for scent marking, to proclaim their territories and prevent intrusion by competitors (*Gazit et al., 1997*). However, mole rat odors may also serve as sexual attractants. Heth and colleagues showed that specific pheromones in urine are important for both courtship and territoriality in males and females (*Heth et al., 1992*). A later study showed that female BMRs were attracted to males with high urinary testosterone levels, suggesting that testosterone and androstenedione behave as pheromones and have an olfactory effect (*Gottreich et al., 2000*). Follow-up studies showed that male BMRs kept in a lab facility have significantly lower androgens, testosterone and androstenedione levels compared to male BMRs in the wild, which might explain their low courtship behavior in the lab and the low breeding success rate in captivity (*Shanas et al., 1995*). Artificially induced estrous female mole rats were shown to be attracted to, and prefer male odors belonging to their chromosomal subspecies when auditory and tactile cues were excluded (*Nevo et al., 1976*). These data support the assumption that pheromones are highly involved in reproductive behavior and genetic speciation of the BMR. The mechanism allowing the mole rat to detects and process pheromone signals is yet to be determined.

Neuromodulation of aggression and social behavior in subterranean mole rats

Various neuromodulators were shown to be involved in aggressive behavior and sociability in mammalian species in general, and in rodent species in particular (*Insel and Young, 2000*; *Lee and Beery, 2019*). In this section, we focus on oxytocin (OT), arginine vasopressin (AVP) and corticotrophin releasing factor (CRF) as three potential hypothalamic neurotransmitters that might be involved in regulation of the unique social behaviors of the BMR. Since very little is known regarding the neurobiology of the BMR, we expended this section to review the accumulating knowledge of other mole rat species, including the eusocial naked and African mole rats, and the solitary Cape mole rat.

Oxytocin and vasopressin

The neuropeptides oxytocin and vasopressin are strongly associated with various social behaviors such as social memory and attachment, sexual and maternal behavior, affiliation and aggression in humans and many other mammalian species (*Anacker and Beery, 2013*; *Kompier et al., 2019*; *Lim and Young, 2006*; *Veenema and Neumann, 2008*). These centrally released neuromodulators regulate neural activity in multiple brain regions involved in social behavior. In the eusocial NMR (*Rosen et al., 2008*) and African Ansell's mole rat (*Valesky et al., 2012*), the majority of OT cells was found in the paraventricular nucleus (PVN) and supraoptic nuclei (SON), similar to many other mammalian species (*Buijs, 1978*; *Dubois-Dauphin et al., 1989*; *Hermes et al., 1988*; *Sofroniew et al., 1979*). Sex differences in the number of OT and AVP neurons were examined in several rodent species and were demonstrated in house mice, Brandt's voles (*Lasiopodomys brandtii*), mandarin voles (*Lasiopodomys mandarinus*) (*Qiao et al., 2013*) and greater long-tailed hamsters (*Tscherskia triton*) (*Häussler et al., 1990*; *Xu et al., 2010*). However, no sexual dimorphism in OT neuron number was found in prairie voles (*Yamamoto et al., 2004*), Ansell's mole rats (*Valesky et al., 2012*), and naked mole rats (*Mooney and Holmes, 2013*).

In the blind mole rat, no data was published thus far regarding the hypothalamic population and distribution of OT neurons. Preliminary data recently established in a comparative study in our lab, found that when considering the differences in brain size, the BMR's PVN contains significantly lower numbers of OT neurons compared to mice. Furthermore, we found no indication of sex differences in the number of OT cells in the PVN of male and female BMRs (unpublished data). Moreover, while it is often assumed that male BMRs are more aggressive than females, our observations suggest similar levels of aggression in both sexes (unpublished data), which might be related to the sex similarities in OT distribution.

There are many evidence that link social cues with the number of OT and AVP cells in the hypothalamus. The presence of a social stimulus was shown to activate the OT system to promote adaptive social behavior responses; a study of the eusocial NMR that examined the effect of social status on the number of OT neurons, revealed that subordinate individuals have more OT-producing neurons in the PVN compared to breeding individuals (*Mooney and Holmes, 2013*). Peripheral administration of OT to the eusocial naked mole rat enhanced social behaviors such as in-colony huddling, time spent in close proximity to a conspecific and the number of its investigations, and this enhancement was blocked by co-administration of an OT antagonist (*Mooney et al., 2014*). This further strengthens the apparent role of oxytocin in the NMR's social behavior. As for the African Ansell's mole rat, no significant differences in OT and AVP neurons were found in individuals from different social and reproductive ranks (*Valesky et al., 2012*).

Oxytocin and vasopressin have been suggested to play a role in the regulation of agonistic, antisocial and aggressive behaviors in various rodents (*Tan et al., 2019*), and were implicated in the manifestation of autism spectrum disorders (ASD). For example, it was recently shown that *Shank3b* KO mice, a common mouse model of ASD, which present abnormal social behaviors, have reduced numbers of OT neurons in the PVN (*Resendez et al., 2020*). While most studies indicate that OT acts as a prosocial agent, reducing aggressiveness (*Calcagnoli et al., 2014*; *Harmon et al., 2002*; *Takayanagi et al., 2005*; *Tsuda et al., 2011*; *Veenema et al., 2007*; *Winslow et al., 2000*), some studies indicate that OT also enhances agonistic and aggressive behaviors (reviewed by [*Beery, 2015*]), mostly maternal aggression (*Bosch et al., 2005*; *Oliveira et al., 2021*, *DeVries et al., 1997*; *Ferris et al., 1992*), but also paternal aggression (*Shabalova et al., 2020*). For AVP, the majority of studies indicate that it is involved in the upregulation of aggressive behavior in rodents. For example, enhanced aggression due to early life stress (ES) was shown to be associated with upregulation of AVP expression in the PVN and SON of male rats (*Veenema et al., 2006*; *Veenema and Neumann, 2009*). On the contrary, mice (*Tsuda et al., 2011*) and mandarin voles (*Wei et al., 2013*) presented decreased aggression after ES, which was accompanied by a decrease in AVP neurons in the PVN. These findings indicate that AVP is a neuromodulator involved in the manifestation of aggressive behavior in rodents. The response of OT and AVP neuronal populations to social stimuli in the blind mole rat was not documented. As far as we know, no attempts were made to administer OT or AVP to BMRs, either centrally or peripherally. In addition to OT and AVP, important findings can arise from exploring their associated receptors in the solitary BMRs, as there are growing evidence for diversity in their genetic regulation, that might trigger variations in social behaviors (*Donaldson and Young, 2008*; *Insel et al., 1991*).

For example, a genetic diversity in the levels of brain AVP receptor in monogamous prairie voles was demonstrated to influence sexual fidelity level in males (*Okhovat et al., 2015*). Expression levels of OT and AVP, both centrally and peripherally, have never been documented in BMRs, and could shed light on the basis of different social behaviors in males and females (for example [*Bendesky et al., 2017*; *Yohn et al., 2017*]). Taking into account findings from other rodents and other mole rat species in particular, we assume that OT and AVP neuronal populations play a key role in regulating social behaviors including aggression and agonistic phenotypes, in the BMR.

Corticotrophin-releasing factor

In the mammalian brain, CRF is most abundant in the PVN, central amygdala (CeA) and hindbrain (*Merchenthaler et al., 1982*). With initiation of the stress response, CRF neurons in the PVN are evoked to release CRF peptide at the median eminence, triggering adrenocorticotropic hormone release from the pituitary, resulting in elevated corticosteroid production from adrenal cells, and the manifestation of different survival behaviors (*Jiang et al., 2019*; *Koob et al., 1994*). In the CNS, CRF and its related peptides- urocortin I-III were shown to be involved in the regulation of social behaviors such as parental care, affiliation and aggression (*Hostetler and Ryabinin, 2013*).

The effects of CRF and its receptors in regulation of male aggression in rodent species depend on the site of its administration, dosage and experimental paradigm. In some studies, CRF administration, or elimination of one of its ligands or receptors (by a genetic knock-out), was shown to facilitate or decrease aggressive behavior (*Breu et al., 2012*; *Coste et al., 2006*; *Elkabir et al., 1990*; *Mele et al., 1987*), while in others, such manipulations had no effect (*Gammie et al., 2005*; *Gammie and Stevenson, 2006*).

In a comparative study, Coen found considerable differences in CRF abundance and receptor binding in the telencephalon, between the eusocial NMR and the solitary Cape mole rat (*Coen et al., 2015*). These differences might reflect the opposite social strategies of the two mole rat species.

Further research into the role of the OT, AVP, and CRF systems in sociability of the solitary BMR, and their comparison to findings in the eusocial NMR, could potentially add to our understanding of the neuromodulators and circuits governing anti-social behavior.

Summary

In his review from 1991, *Heiligenberg, 1991* discussed the different approaches used by scientists in the study of the neural basis of animal behavior, and described how often times, neuroethologists choose 'champion species' for their studies. These 'champion species' possess unique aspects of sensory or motor performance, that are linked to specialized neuronal structures in the CNS (*Heiligenberg, 1991*). Here we argue that the blind mole rat qualifies as a champion species in terms of its sensory performance, behavioral repertoire and special adaptations to underground life, which manifest in remarkable brain plasticity.

Being congenitally blind, *Spalax ehrenbergi* is deprived of visual inputs, and thus compensates via the diversion of the visual modality to the auditory modality. Cross-modal neuroplasticity in animal models is induced, in most cases, by experimental procedures (*Izraeli et al., 2002*; *Rauschecker and Kniepert, 1994*; *Toldi et al., 1994a*; *Toldi et al., 1994b*; *Yaka et al., 2000*). By using the blind mole rat as a model animal, we take advantage of its natural and congenital sensory deficit- its blindness.

Neuroscience and social behavior research has been, and still is, mostly conducted using highly social animal models, most commonly mice and rats (for example [*Ellenbroek and Youn, 2016*; *Haney et al., 1989*; *Karamihalev et al., 2020*; *Scott et al., 2015*; *Shemesh et al., 2013*]). Neuroethological studies have also been conducted on other rodent species, such as golden hamsters (*Bunnell et al., 1970*), prairie voles (*McGraw and Young, 2010*), gerbils (*Martínez et al., 2019*) and in the subterranean niche, the naked mole rat is a relatively common subject for research, being eusocial and easy to breed in captivity (*Buffenstein et al., 2021*). However, the blind mole rat is territorial and aggressive, and is extremely difficult to breed in the lab. It has been shown once that under careful conditions, the BMR can be bred in captivity (*Gazit et al., 1996*; *Figure 3*), nevertheless, as of yet no major breeding programs have been initiated. To our knowledge, there is no known way to determine the age of an adult BMR captured in the field, which adds to the uncontrolled variables involved in BMR research. Still, *Spalacinae* are very common in some regions, and research has been conducted successfully on wild-caught individuals (for example *Gazit and Terkel, 1998*; *Gazit and Terkel, 2000*; *Kimchi*

et al., 2004; *Kimchi and Terkel, 2001*; *Nevo et al., 1975*; *Figure 3A*). Furthermore, no genetic manipulations or selective breeding are done on BMRs, and thus all naturally occurring properties and genetically determined mechanisms are conserved in this non-model organism. This is in contrast to laboratory mice and rats, which are subjected to generations of domestication and inbreeding, thus accumulating numerous mutations and consequently present many atypical features compared to wild populations in nature. Many natural behaviors of BMRs can and have been addressed in lab and semi-natural behavioral experimental setups related to the sensory systems outlined above (for example *Zenuto et al., 2001*; *Figure 3*). However, as in mice and rats, it is best to complement lab studies with natural experiments from a behavioral ecology approach, to collect the full suite of complex behaviors in the BMR.

In conclusion, a handful of animal models for the study of diverse biology and neurobiology is not sufficient. We have recently discussed the main biases in social behavioral research, and showed that science in general, and behavioral and neurobiological studies in particular, tend to rely mostly on male mice in a small confined laboratory environment (*Zilkha et al., 2016*). However, in order to understand the neural mechanisms underlying different types of social behaviors, non-traditional model organisms must be considered. The blind mole rat provides an excellent non-traditional model, whose neuroethology might also shed light on the neurobiological basis of social deficits in humans. Moreover, BMRs provides an almost untouched territory in the neuroscience field, rendering them a fascinating and exciting model organism for neuroethological research. Nevertheless, in order to utilize the unique features of BMRs in our studies and establish it as a new model in social neurosciences, some basic genetic, molecular and neurological data needs to be collected. A *Spalax ehrenbergi* genomic assembly has been deposited for a single female BMR (*Fang et al., 2014*). In addition, transcriptomic sequencing analyses have uncovered differential expression profiles in BMRs under different conditions related to underground stressors (*Fang et al., 2014*; *Malik et al., 2011*), and scRNA sequencing of microglia revealed similarities of BMRs to other rodents (*Geirsdottir et al., 2019*). An additional step forward would be mapping of the BMR's brain morphology and functional circuits. This can be done by detailed histological analyses, accompanied by MRI. Furthermore, making commonly used viral tools for neural manipulations applicable for BMRs will assist in mapping the cascades underlying brain coding of social information. Recently, Hadi and colleagues demonstrated a promising breakthrough in the field of genetic engineering in mole rats, reporting a successful transformation of NMR cells, using a novel CRISPR gRNA library and lentiviral vectors (*Hadi, 2020a*; *Hadi et al., 2020b*). This is a major step forward in advancing the genetic tools used on subterranean rodents, and making them much more available for the research of mole rats in general, and the blind mole rat in particular.

Acknowledgements

Additional information

Author contributions

Yael Kashash, Grace Smarsh, Noga Zilkha, Conceptualization, Writing – original draft, Writing – review and editing; Yossi Yovel, Supervision, Writing – original draft; Tali Kimchi, Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review and editing

Author ORCIDs
Yael Kashash http://orcid.org/0000-0002-1869-5221
Noga Zilkha http://orcid.org/0000-0003-4650-766X
Tali Kimchi http://orcid.org/0000-0001-7059-1545

References

Addison WHF, Rademaker LA. 1927. The postnatal growth of the vomeronasal organ of the albino rat (Mus norvegicus albinus). *The Journal of Comparative Neurology* **44**:69–86. DOI: https://doi.org/10.1002/cne.900440105

Anacker AMJ, Beery AK. 2013. Life in groups: the roles of oxytocin in mammalian sociality. *Frontiers in Behavioral Neuroscience* **7**:185. DOI: https://doi.org/10.3389/fnbeh.2013.00185, PMID: 24376404

Azevedo J, Vieira-Coelho M, Castelo-Branco M, Coelho R, Figueiredo-Braga M. 2020. Impulsive and premeditated aggression in male offenders with antisocial personality disorder. *PLOS ONE* **15**:e0229876. DOI: https://doi.org/10.1371/journal.pone.0229876, PMID: 32142531

Babb SJ, Crystal JD. 2006. Discrimination of what, when, and where is not based on time of day. *Learning & Behavior* **34**:124–130. DOI: https://doi.org/10.3758/BF03193188

Balemans MG, Pévet P, Legerstee WC, Nevo E. 1980. Preliminary investigations of melatonin and 5-methoxy-tryptophol synthesis in the pineal, retina, and harderian gland of the mole rat and in the pineal of the mouse "eyeless." *Journal of Neural Transmission* **49**:247–255. DOI: https://doi.org/10.1007/BF01252129, PMID: 7463037

Barker AJ, Koch U, Lewin GR, Pyott SJ. 2021a. Hearing and vocalizations in the naked mole-rat. Buffenstein R, Park TJ, Holmes MM (Eds). *The Extraordinary Biology of the Naked Mole-Rat*. Cham: Springer. p. 157–195. DOI: https://doi.org/10.1007/978-3-030-65943-1_6

Barker AJ, Veviurko G, Bennett NC, Hart DW, Mograby L, Lewin GR. 2021b. Cultural transmission of vocal dialect in the naked mole-rat. *Science* **371**:503–507. DOI: https://doi.org/10.1126/science.abc6588, PMID: 33510025

Bednářová R, Hrouzková-Knotková E, Burda H, Sedláček F, Šumbera R. 2013. Vocalizations of the giant mole-rat (*Fukomys mechowii*), a subterranean rodent with the richest vocal repertoire. *Bioacoustics* **22**:87–107. DOI: https://doi.org/10.1080/09524622.2012.712749

Beery AK. 2015. Antisocial oxytocin: complex effects on social behavior. *Current Opinion in Behavioral Sciences* **6**:174–182. DOI: https://doi.org/10.1016/j.cobeha.2015.11.006

Begall S, Burda H, Schleich CE. 2007. Subterranean Rodents: News from Underground. Begall S, Burda H, Schleich CE (Eds). *Subterranean Rodents*. Berlin, Heidelberg: Springer. p. 3–9. DOI: https://doi.org/10.1007/978-3-540-69276-8_1

Begall S, Burda H, Malkemper EP. 2014. Magnetoreception in mammals. *Advances in the Study of Behavior* **46**:45–88. DOI: https://doi.org/10.1016/B978-0-12-800286-5.00002-X

Bendesky A, Kwon Y-M, Lassance J-M, Lewarch CL, Yao S, Peterson BK, He MX, Dulac C, Hoekstra HE. 2017. The genetic basis of parental care evolution in monogamous mice. *Nature* **544**:434–439. DOI: https://doi.org/10.1038/nature22074, PMID: 28424518

Bennett NC, Jarvis JUM. 1988. The Social Structure and Reproductive Biology of Colonies of the Mole-Rat, Cryptomys damarensis (Rodentia, Bathyergidae). *Journal of Mammalogy* **69**:293–302. DOI: https://doi.org/10.2307/1381379

Bennett NC, Faulkes CG. 2000. African Mole-Rats: Ecology and Eusociality. Cambridge University Press.

Bosch OJ, Meddle SL, Beiderbeck DI, Douglas AJ, Neumann ID. 2005. Brain oxytocin correlates with maternal aggression: link to anxiety. *The Journal of Neuroscience* **25**:6807–6815. DOI: https://doi.org/10.1523/JNEUROSCI.1342-05.2005, PMID: 16033890

Bradbury J, Vehrencamp S. 2011. Principles of animal communication, 2nd edn. Sunderland, Mass : Sinauer Associates.

Breitenmoser-Würsten C, Zimmermann F, Molinari-Jobin A, Molinari P, Capt S, Vandel J-M, Stahl P, Breitenmoser U. 2007. Spatial and Social stability of a Eurasian lynx Lynx lynx population: an assessment of 10 years of observation in the Jura Mountains. *Wildlife Biology* **13**:365–380. DOI: https://doi.org/10.2981/0909-6396(2007)13[365:SASSOA]2.0.CO;2

Brenowitz EA, Zakon HH. 2015. Emerging from the bottleneck: benefits of the comparative approach to modern neuroscience. *Trends in Neurosciences* **38**:273–278. DOI: https://doi.org/10.1016/j.tins.2015.02.008, PMID: 25800324

Breu J, Touma C, Hölter SM, Knapman A, Wurst W, Deussing JM. 2012. Urocortin 2 modulates aspects of social behaviour in mice. *Behavioural Brain Research* **233**:331–336. DOI: https://doi.org/10.1016/j.bbr.2012.05.031, PMID: 22640813

Bronchti G, Heil P, Scheich H, Wollberg Z. 1989. Auditory pathway and auditory activation of primary visual targets in the blind mole rat (Spalax ehrenbergi): I. 2-deoxyglucose study of subcortical centers. *The Journal of Comparative Neurology* **284**:253–274. DOI: https://doi.org/10.1002/cne.902840209

Bronchti G, Heil P, Sadka R, Hess A, Scheich H, Wollberg Z. 2002. Auditory activation of "visual" cortical areas in the blind mole rat (Spalax ehrenbergi). *The European Journal of Neuroscience* **16**:311–329. DOI: https://doi.org/10.1046/j.1460-9568.2002.02063.x, PMID: 12169112

Bronson FH. 1979. The Reproductive Ecology of the House Mouse. *The Quarterly Review of Biology* **54**:265–299. DOI: https://doi.org/10.1086/411295, PMID: 390600

Brückmann G, Burda H. 1997. Hearing in blind subterranean Zambian mole-rats (Cryptomys sp.): collective behavioural audiogram in a highly social rodent. *Journal of Comparative Physiology A* **181**:83–88. DOI: https://doi.org/10.1007/s003590050095, PMID: 9216072

Budinger E, Heil P, Hess A, Scheich H. 2006. Multisensory processing via early cortical stages: Connections of the primary auditory cortical field with other sensory systems. *Neuroscience* **143**:1065–1083. DOI: https://doi.org/10.1016/j.neuroscience.2006.08.035, PMID: 17027173

Buffenstein R, Park TJ, Holmes MM. 2021. The Extraordinary Biology of the Naked Mole-Rat. Cham: Springer.DOI: https://doi.org/10.1007/978-3-030-65943-1

Buijs RM. 1978. Intra- and extrahypothalamic vasopressin and oxytocin pathways in the rat. *Cell and Tissue Research* **192**:423–435. DOI: https://doi.org/10.1007/BF00212323, PMID: 699026

Bunnell BN, Sodetz FJ, Shalloway DI. 1970. Amygdaloid lesions and social behavior in the golden hamster. *Physiology & Behavior* **5**:153–161. DOI: https://doi.org/10.1016/0031-9384(70)90059-4, PMID: 5535792

Burda H. 2006. Ear and eye in subterranean mole-rats, Fukomys anselli (Bathyergidae) and Spalax ehrenbergi (Spalacidae): progressive specialisation or regressive degeneration? *Animal Biology* **56**:475–486. DOI: https://doi.org/10.1163/157075606778967847

Calcagnoli F, de Boer SF, Beiderbeck DI, Althaus M, Koolhaas JM, Neumann ID. 2014. Local oxytocin expression and oxytocin receptor binding in the male rat brain is associated with aggressiveness. *Behavioural Brain Research* **261**:315–322. DOI: https://doi.org/10.1016/j.bbr.2013.12.050, PMID: 24406721

Campi KL, Bales KL, Grunewald R, Krubitzer L. 2010. Connections of auditory and visual cortex in the prairie vole (Microtus ochrogaster): evidence for multisensory processing in primary sensory areas. *Cerebral Cortex* **20**:89–108. DOI: https://doi.org/10.1093/cercor/bhp082, PMID: 19395525

Capranica R, Nevo E, Moffat A. 1974. Vocal repertoire of a subterranean rodent (Spalax). *The Journal of the Acoustical Society of America* **55**:e481. DOI: https://doi.org/10.1121/1.3438017

Caspar KR, Moldenhauer K, Moritz RE, Němec P, Malkemper EP, Begall S. 2020. Eyes are essential for magnetoreception in a mammal. *Journal of the Royal Society, Interface* **17**:e20200513. DOI: https://doi.org/10.1098/rsif.2020.0513, PMID: 32993431

Catania KC, Remple MS. 2002. Somatosensory cortex dominated by the representation of teeth in the naked mole-rat brain. *PNAS* **99**:5692–5697. DOI: https://doi.org/10.1073/pnas.072097999, PMID: 11943853

Cernuda-Cernuda R, DeGrip WJ, Cooper HM, Nevo E, Garcia-Fernandez JM. 2002. The retina of Spalax ehrenbergi: Novel histologic features supportive of a modified photosensory role. *Investigative Ophthalmology & Visual Science* **43**:2374–2383.

Coen CW, Kalamatianos T, Oosthuizen MK, Poorun R, Faulkes CG, Bennett NC. 2015. Sociality and the telencephalic distribution of corticotrophin-releasing factor, urocortin 3, and binding sites for CRF type 1 and type 2 receptors: A comparative study of eusocial naked mole-rats and solitary Cape mole-rats. *Journal of Comparative Neurology* **523**:2344–2371. DOI: https://doi.org/10.1002/cne.23796

Cooper HM, Herbin M, Nevo E. 1993a. Ocular regression conceals adaptive progression of the visual system in a blind subterranean mammal. *Nature* **361**:156–159. DOI: https://doi.org/10.1038/361156a0

Cooper HM, Herbin M, Nevo E. 1993b. Visual system of a naturally microphthalmic mammal: The blind mole rat,Spalax ehrenbergi. *The Journal of Comparative Neurology* **328**:313–350. DOI: https://doi.org/10.1002/cne.903280302, PMID: 8440785

Costanzo MS, Bennett NC, Lutermann H. 2009. Spatial learning and memory in African mole-rats: The role of sociality and sex. *Physiology & Behavior* **96**:128–134. DOI: https://doi.org/10.1016/j.physbeh.2008.09.008, PMID: 18824187

Coste SC, Heard AD, Phillips TJ, Stenzel-Poore MP. 2006. Corticotropin-releasing factor receptor type 2-deficient mice display impaired coping behaviors during stress. *Genes, Brain and Behavior* **5**:131–138. DOI: https://doi.org/10.1111/j.1601-183X.2005.00142.x, PMID: 16507004

Cross SKJ, Martin YH, Salia S, Gamba I, Major CA, Hassan S, Parsons KA, Swift-Gallant A. 2020. Puberty is a Critical Period for Vomeronasal Organ Mediation of Socio-sexual Behavior in Mice. *Frontiers in Behavioral Neuroscience* **14**:e606788. DOI: https://doi.org/10.3389/fnbeh.2020.606788, PMID: 33551763

Cummings ME, Ramsey ME. 2015. Mate choice as social cognition: predicting female behavioral and neural plasticity as a function of alternative male reproductive tactics. *Current Opinion in Behavioral Sciences* **6**:125–131. DOI: https://doi.org/10.1016/j.cobeha.2015.10.001

David-Gray ZK, Janssen JW, DeGrip WJ, Nevo E, Foster RG. 1998. Light detection in a "blind" mammal. *Nature Neuroscience* **1**:655–656. DOI: https://doi.org/10.1038/3656, PMID: 10196579

David-Gray ZK, Cooper HM, Janssen JW, Nevo E, Foster RG. 1999. Spectral tuning of a circadian photopigment in a subterranean "blind" mammal (Spalax ehrenbergi. *FEBS Letters* **461**:343–347. DOI: https://doi.org/10.1016/s0014-5793(99)01455-6, PMID: 10567724

David-Gray ZK, Bellingham J, Munoz M, Avivi A, Nevo E, Foster RG. 2002. Adaptive loss of ultraviolet-sensitive/violet-sensitive (UVS/VS) cone opsin in the blind mole rat (Spalax ehrenbergi. *The European Journal of Neuroscience* **16**:1186–1194. DOI: https://doi.org/10.1046/j.1460-9568.2002.02161.x, PMID: 12405979

Dennis JC, Stilwell NK, Smith TD, Park TJ, Bhatnagar KP, Morrison EE. 2020. Is the Mole Rat Vomeronasal Organ Functional? *Anatomical Record* **303**:318–329. DOI: https://doi.org/10.1002/ar.24060, PMID: 30614661

Dent ML, Screven LA, Kobrina A. 2018. Hearing in Rodents. Dent ML, FayRR, Popper AN (Eds). *Rodent Bioacoustics.* Cham: Springer. p. 71–105. DOI: https://doi.org/10.1007/978-3-319-92495-3

DeVries AC, Young WS, Nelson RJ. 1997. Reduced aggressive behaviour in mice with targeted disruption of the oxytocin gene. *Journal of Neuroendocrinology* 9:363–368. DOI: https://doi.org/10.1046/j.1365-2826.1997.t01-1-00589.x, PMID: 9181490

Donaldson ZR, Young LJ. 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 322:900–904. DOI: https://doi.org/10.1126/science.1158668, PMID: 18988842

Doty RL. 1986. Odor-guided behavior in mammals. *Experientia* 42:257–271. DOI: https://doi.org/10.1007/BF01942506, PMID: 3514263

Du Toit JT, Jarvis JUM, Louw GN. 1985. Nutrition and burrowing energetics of the Cape mole-rat Georychus capensis. *Oecologia* 66:81–87. DOI: https://doi.org/10.1007/BF00378556, PMID: 28310816

Dubois-Dauphin M, Tribollet E, Dreifuss JJ. 1989. Distribution of neurohypophysial peptides in the guinea pig brain. II. An immunocytochemical study of oxytocin. *Brain Research* 496:66–81. DOI: https://doi.org/10.1016/0006-8993(89)91052-4

Dutton DG, Karakanta C. 2013. Depression as A risk marker for aggression: A critical review. *Aggression and Violent Behavior* 18:310–319. DOI: https://doi.org/10.1016/j.avb.2012.12.002

Elkabir DR, Wyatt ME, Vellucci SV, Herbert J. 1990. The effects of separate or combined infusions of corticotrophin-releasing factor and vasopressin either intraventricularly or into the amygdala on aggressive and investigative behaviour in the rat. *Regulatory Peptides* 28:199–214. DOI: https://doi.org/10.1016/0167-0115(90)90018-r, PMID: 2343163

Ellenbroek B, Youn J. 2016. Rodent models in neuroscience research: is it a rat race? *Disease Models & Mechanisms* 9:1079–1087. DOI: https://doi.org/10.1242/dmm.026120

Esquiva G, Avivi A, Hannibal J. 2016. Non-image Forming Light Detection by Melanopsin, Rhodopsin, and Long-Middlewave (L/W) Cone Opsin in the Subterranean Blind Mole Rat, Spalax Ehrenbergi: Immunohistochemical Characterization, Distribution, and Connectivity. *Frontiers in Neuroanatomy* 10:e61. DOI: https://doi.org/10.3389/fnana.2016.00061, PMID: 27375437

Fang X, Nevo E, Han L, Levanon EY, Zhao J, Avivi A, Larkin D, Jiang X, Feranchuk S, Zhu Y, Fishman A, Feng Y, Sher N, Xiong Z, Hankeln T, Huang Z, Gorbunova V, Zhang L, Zhao W, Wildman DE, et al. 2014. Genome-wide adaptive complexes to underground stresses in blind mole rats Spalax. *Nature Communications* 5:e3966. DOI: https://doi.org/10.1038/ncomms4966, PMID: 24892994

Ferris CF, Foote KB, Meltser HM, Plenby MG, Smith KL, Insel TR. 1992. Oxytocin in the Amygdala Facilitates Maternal Aggression. *Annals of the New York Academy of Sciences* 652:456–457. DOI: https://doi.org/10.1111/j.1749-6632.1992.tb34382.x, PMID: 1626847

Follett BK. 2015. "Seasonal changes in the neuroendocrine system": Some reflections. *Frontiers in Neuroendocrinology* 37:3–12. DOI: https://doi.org/10.1016/j.yfrne.2014.11.003, PMID: 25462591

Freedman MS, Lucas RJ, Soni B, von Schantz M, Muñoz M, David-Gray Z, Foster R. 1999. Regulation of Mammalian Circadian Behavior by Non-rod, Non-cone, Ocular Photoreceptors. *Science* 284:502–504. DOI: https://doi.org/10.1126/science.284.5413.502, PMID: 10205061

Galil J. 1967. On the Dispersal of the Bulbs of Oxalis Cernua Thunb. By Mole-Rats (Spalax Ehrenbergi Nehring. *The Journal of Ecology* 55:e787. DOI: https://doi.org/10.2307/2258425

Galland P, Pazur A. 2005. Magnetoreception in plants. *Journal of Plant Research* 118:371–389. DOI: https://doi.org/10.1007/s10265-005-0246-y, PMID: 16283069

Gammie SC, Hasen NS, Stevenson SA, Bale TL, D'Anna KL. 2005. Elevated stress sensitivity in corticotropin-releasing factor receptor 2 deficient mice decreases maternal, but not intermale aggression. *Behavioural Brain Research* 160:169–177. DOI: https://doi.org/10.1016/j.bbr.2004.11.026, PMID: 15836912

Gammie SC, Stevenson SA. 2006. Intermale aggression in corticotropin-releasing factor receptor 1 deficient mice. *Behavioural Brain Research* 171:63–69. DOI: https://doi.org/10.1016/j.bbr.2006.03.017, PMID: 16621057

Gao F, Li T, Hu J, Zhou X, Wu J, Wu Q. 2016. Comparative analysis of three purification protocols for retinal ganglion cells from rat. *Molecular Vision* 22:387–400 PMID: 27122968.,

Gazit I, Shanas U, Terkel J. 1996. First successful breeding of the blind mole rat (Spalax ehrenbergi) in captivity. *Israel Journal of Ecology and Evolution* 42:3–13. DOI: https://doi.org/10.1080/00212210.1996.10688829

Gazit I, Terkel J, Zuri I. 1997. Effect of Scent-Marking in Delaying Territorial Invasion in the Blind Mole-Rat Spalax Ehrenbergi. *Behaviour* 134:867–880. DOI: https://doi.org/10.1163/156853997X00197

Gazit I, Terkel J. 1998. Chronological development of behavior in the blind mole rat (Spalax ehrenbergi. *International Journal of Comparative Psychology* 11.

Gazit I, Terkel J. 2000. Reproductive behavior of the blind mole-rat (*Spalax ehrenbergi*) in a seminatural burrow system . *Canadian Journal of Zoology* 78:570–577. DOI: https://doi.org/10.1139/z99-251

Geirsdottir L, David E, Keren-Shaul H, Weiner A, Bohlen SC, Neuber J, Balic A, Giladi A, Sheban F, Dutertre C-A, Pfeifle C, Peri F, Raffo-Romero A, Vizioli J, Matiasek K, Scheiwe C, Meckel S, Mätz-Rensing K, van der Meer F, Thormodsson FR, et al. 2019. Cross-Species Single-Cell Analysis Reveals Divergence of the Primate Microglia Program. *Cell* 179:1609–1622. DOI: https://doi.org/10.1016/j.cell.2019.11.010, PMID: 31835035

Gerhardt P, Henning Y, Begall S, Malkemper EP. 2017. Correction: Audiograms of three subterranean rodent species (genus Fukomys) determined by auditory brainstem responses reveal extremely poor high-frequency cut-offs. *The Journal of Experimental Biology* 220:e4747. DOI: https://doi.org/10.1242/jeb.175190, PMID: 29237771

Gilad E, Shanas U, Terkel J, Zisapel N. 1997. Putative melatonin receptors in the blind mole rat Harderian gland. *The Journal of Experimental Zoology* 277:435–441. DOI: https://doi.org/10.1002/(SICI)1097-010X(19970415)277:6<435::AID-JEZ3>3.0.CO;2-P

Gilley DW, Wilson RS, Beckett LA, Evans DA. 1997. Psychotic Symptoms and Physically Aggressive Behavior in Alzheimer's Disease. *Journal of the American Geriatrics Society* **45**:1074–1079. DOI: https://doi.org/10.1111/j.1532-5415.1997.tb05969.x, PMID: 9288014

Gottreich A, Zuri I, Barel S, Hammer I, Terkel J. 2000. Urinary testosterone levels in the male blind mole rat (Spalax ehrenbergi) affect female preference. *Physiology & Behavior* **69**:309–315. DOI: https://doi.org/10.1016/S0031-9384(99)00249-8, PMID: 10869597

Gottreich A, Zuri I, Hammel I, Terkel J. 2001. Noninvolvement of testosterone in aggressive defense behavior in the male blind mole ratSpalax ehrenbergi. *Aggressive Behavior* **27**:64–72. DOI: https://doi.org/10.1002/1098-2337(20010101/31)27:1<64::AID-AB6>3.0.CO;2-C

Guttman R, Naftali G, Nevo E. 1975. Aggression patterns in three chromosome forms of the mole rat, Spalax ehrenbergi. *Animal Behaviour* **23**:485–493. DOI: https://doi.org/10.1016/0003-3472(75)90124-4, PMID: 1172395

Hadi F. 2020a. Understanding the Cancer Resistance Mechanisms of the Naked Mole-Rat. University of Cambridge Press.

Hadi F, Kulaberoglu Y, Lazarus KA, Bach K, Ugur R, Beattie P, Smith ESJ, Khaled WT. 2020b. Transformation of naked mole-rat cells. *Nature* **583**:E1–E7. DOI: https://doi.org/10.1038/s41586-020-2410-x, PMID: 32612221

Haim A, Heth G, Pratt H, Nevo E. 1983. Photoperiodic effects on thermoregulation in a 'blind' subterranean mammal. *Journal of Experimental Biology* **107**:59–64. DOI: https://doi.org/10.1242/jeb.107.1.59

Hale ME. 2019. Toward Diversification of Species Models in Neuroscience. *Brain, Behavior and Evolution* **93**:166–168. DOI: https://doi.org/10.1159/000500499, PMID: 31416090

Halpern M, Martınez-Marcos A. 2003. Structure and function of the vomeronasal system: an update. *Progress in Neurobiology* **70**:245–318. DOI: https://doi.org/10.1016/S0301-0082(03)00103-5, PMID: 12951145

Haney M, Debold JF, Miczek KA. 1989. Maternal aggression in mice and rats towards male and female conspecifics. *Aggressive Behavior* **15**:443–453. DOI: https://doi.org/10.1002/1098-2337(1989)15:6<443::AID-AB2480150605>3.0.CO;2-U

Hannibal J. 2002. Neurotransmitters of the retino-hypothalamic tract. *Cell and Tissue Research* **309**:73–88. DOI: https://doi.org/10.1007/s00441-002-0574-3, PMID: 12111538

Hannibal J. 2021. Comparative Neurology of Circadian Photoreception: The Retinohypothalamic Tract (RHT) in Sighted and Naturally Blind Mammals. *Frontiers in Neuroscience* **15**:e640113. DOI: https://doi.org/10.3389/fnins.2021.640113, PMID: 34054403

Harmon AC, Huhman KL, Moore TO, Albers HE. 2002. Oxytocin inhibits aggression in female Syrian hamsters. *Journal of Neuroendocrinology* **14**:963–969. DOI: https://doi.org/10.1046/j.1365-2826.2002.00863.x, PMID: 12472877

Häussler HU, Jirikowski GF, Caldwell JD. 1990. Sex differences among oxytocin-immunoreactive neuronal systems in the mouse hypothalamus. *Journal of Chemical Neuroanatomy* **3**:271–276 PMID: 2204355.,

He K, Liu Q, Xu DM, Qi FY, Bai J, He SW, Chen P, Zhou X, Cai WZ, Chen ZZ, Liu Z, Jiang XL, Shi P. 2021. Echolocation in soft-furred tree mice. *Science* **372**:eaay1513. DOI: https://doi.org/10.1126/science.aay1513, PMID: 34140356

Heffner H, Masterton B. 1980. Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. *The Journal of the Acoustical Society of America* **68**:1584–1599. DOI: https://doi.org/10.1121/1.385213

Heffner RS, Heffner HE. 1990. Vestigial hearing in a fossorial mammal, the pocket gopher (Geomys bursarius. *Hearing Research* **46**:239–252. DOI: https://doi.org/10.1016/0378-5955(90)90005-a, PMID: 2394636

Heffner RS, Heffner HE. 1992. Hearing and sound localization in blind mole rats (Spalax ehrenbergi. *Hearing Research* **62**:206–216. DOI: https://doi.org/10.1016/0378-5955(92)90188-s, PMID: 1429264

Heffner RS, Heffner HE. 1993. Degenerate hearing and sound localization in naked mole rats (Heterocephalus glaber), with an overview of central auditory structures. *The Journal of Comparative Neurology* **331**:418–433. DOI: https://doi.org/10.1002/cne.903310311, PMID: 8514919

Heil P, Bronchti G, Wollberg Z, Scheich H. 1991. Invasion of visual cortex by the auditory system in the naturally blind mole rat. *NeuroReport* **2**:735–738. DOI: https://doi.org/10.1097/00001756-199112000-00001

Heiligenberg W. 1991. The neural basis of behavior: a neuroethological view. *Annual Review of Neuroscience* **14**:247–267. DOI: https://doi.org/10.1146/annurev.ne.14.030191.001335, PMID: 2031571

Hermes M, Buijs RM, Masson-Pévet M, Pévet P. 1988. Oxytocinergic innervation of the brain of the garden dormouse (Eliomys quercinus L). *The Journal of Comparative Neurology* **273**:252–262. DOI: https://doi.org/10.1002/cne.902730209, PMID: 3417903

Heth G, Frankenberg E, Nevo E. 1986. Adaptive optimal sound for vocal communication in tunnels of a subterranean mammal (Spalax ehrenbergi. *Experientia* **42**:1287–1289. DOI: https://doi.org/10.1007/BF01946426, PMID: 3780955

Heth G, Frankenberg E, Raz A, Nevo E. 1987. Vibrational communication in subterranean mole rats (Spalax ehrenbergi). *Behavioral Ecology and Sociobiology* **21**:31–33. DOI: https://doi.org/10.1007/BF00324432

Heth G, Frankenberg E, Nevo E. 1988. "Courtship" Call of Subterranean Mole Rats (Spalax ehrenbergi): Physical Analysis. *Journal of Mammalogy* **69**:121–125. DOI: https://doi.org/10.2307/1381755

Heth G. 1989. Burrow patterns of the mole rat Spalax ehrenbergi in two soil types (terra-rossa and rendzina) in Mount Carmel, Israel. *Journal of Zoology* **217**:39–56. DOI: https://doi.org/10.1111/j.1469-7998.1989.tb02473.x

Heth G, Nevo E, Ikan R, Weinstein V, Ravid U, Duncan H. 1992. Differential olfactory perception of enantiomeric compounds by blind subterranean mole rats (Spalax ehrenbergi). *Experientia* **48**:897–902. DOI: https://doi.org/10.1007/BF02118430, PMID: 1397188

Heth G, Todrank J, Begall S, Koch R, Zilbiger Y, Nevo E, Braude S, Burda H. 2002. Odours underground: subterranean rodents may not forage "blindly." *Behavioral Ecology and Sociobiology* **52**:53–58. DOI: https://doi.org/10.1007/s00265-002-0476-0

Heth G, Todrank J. 2007. Using Odors Underground. Heth G (Ed). *Subterranean Rodents*. Berlin, Heidelberg: Springer. p. 85–96. DOI: https://doi.org/10.1007/978-3-540-69276-8_8

Hill PSM. 2001. Vibration and Animal Communication: A Review. *American Zoologist* **41**:1135–1142. DOI: https://doi.org/10.1093/icb/41.5.1135

Hill PSM. 2009. How do animals use substrate-borne vibrations as an information source? *Die Naturwissenschaften* **96**:1355–1371. DOI: https://doi.org/10.1007/s00114-009-0588-8, PMID: 19593539

Hostetler CM, Ryabinin AE. 2013. The CRF system and social behavior: a review. *Frontiers in Neuroscience* **7**:e92. DOI: https://doi.org/10.3389/fnins.2013.00092, PMID: 23754975

Hrouzková E, Šklíba J, Pleštilová L, Hua L, Meheretu Y. 2018. Seismic communication in spalacids: signals in the giant root-rat and Gansu zokor. *Hystrix, the Italian Journal of Mammalogy* **29**:243–245.

Hsu CY, Li CW. 1994. Magnetoreception in honeybees. *Science* **265**:95–97. DOI: https://doi.org/10.1126/science.265.5168.95, PMID: 17774695

Insel TR, Gelhard R, Shapiro LE. 1991. The comparative distribution of forebrain receptors for neurohypophyseal peptides in monogamous and polygamous mice. *Neuroscience* **43**:623–630. DOI: https://doi.org/10.1016/0306-4522(91)90321-e, PMID: 1656322

Insel TR, Young LJ. 2000. Neuropeptides and the evolution of social behavior. *Current Opinion in Neurobiology* **10**:784–789. DOI: https://doi.org/10.1016/s0959-4388(00)00146-x, PMID: 11240290

Izraeli R, Koay G, Lamish M, Heicklen-Klein AJ, Heffner HE, Heffner RS, Wollberg Z. 2002. Cross-modal neuroplasticity in neonatally enucleated hamsters: structure, electrophysiology and behaviour. *The European Journal of Neuroscience* **15**:693–712. DOI: https://doi.org/10.1046/j.1460-9568.2002.01902.x, PMID: 11886450

Jiang Z, Rajamanickam S, Justice NJ. 2019. CRF signaling between neurons in the paraventricular nucleus of the hypothalamus (PVN) coordinates stress responses. *Neurobiology of Stress* **11**:e100192. DOI: https://doi.org/10.1016/j.ynstr.2019.100192, PMID: 31516918

Jiao H, Hong W, Nevo E, Li K, Zhao H. 2019. Convergent reduction of V1R genes in subterranean rodents. *BMC Evolutionary Biology* **19**:1–9. DOI: https://doi.org/10.1186/s12862-019-1502-4, PMID: 31470793

Karamihalev S, Brivio E, Flachskamm C, Stoffel R, Schmidt MV, Chen A. 2020. Social dominance mediates behavioral adaptation to chronic stress in a sex-specific manner. *eLife* **9**:e58723. DOI: https://doi.org/10.7554/eLife.58723, PMID: 33034286

Kavaliers M, Choleris E. 2017. Social Cognition and the Neurobiology of Rodent Mate Choice. *Integrative and Comparative Biology* **57**:846–856. DOI: https://doi.org/10.1093/icb/icx042, PMID: 28992230

Kelliher KR. 2007. The combined role of the main olfactory and vomeronasal systems in social communication in mammals. *Hormones and Behavior* **52**:561–570. DOI: https://doi.org/10.1016/j.yhbeh.2007.08.012, PMID: 17959176

Keverne EB. 1999. The vomeronasal organ. *Science* **286**:716–720. DOI: https://doi.org/10.1126/science.286.5440.716, PMID: 10531049

Kimchi T, Terkel J. 2000. Importance of touch for the blind mole rat (Spalax ehrenbergi) in learning a complex maze. *Israel J Zool* **46**:e165.

Kimchi T, Terkel J. 2001. Magnetic compass orientation in the blind mole rat Spalax ehrenbergi. *The Journal of Experimental Biology* **204**:751–758. DOI: https://doi.org/10.1242/jeb.204.4.751, PMID: 11171357

Kimchi T, Terkel J. 2002. Seeing and not seeing. *Current Opinion in Neurobiology* **12**:728–734. DOI: https://doi.org/10.1016/s0959-4388(02)00381-1, PMID: 12490266

Kimchi T, Terkel J. 2003a. Detours by the blind mole-rat follow assessment of location and physical properties of underground obstacles. *Animal Behaviour* **66**:885–891. DOI: https://doi.org/10.1006/anbe.2003.2267

Kimchi T, Terkel J. 2003b. Mole rats (Spalax ehrenbergi) select bypass burrowing strategies in accordance with obstacle size. *Die Naturwissenschaften* **90**:36–39. DOI: https://doi.org/10.1007/s00114-002-0383-2

Kimchi T, Etienne AS, Terkel J. 2004. A subterranean mammal uses the magnetic compass for path integration. *PNAS* **101**:1105–1109. DOI: https://doi.org/10.1073/pnas.0307560100, PMID: 14732687

Kimchi T, Terkel J. 2004. Comparison of the role of somatosensory stimuli in maze learning in a blind subterranean rodent and a sighted surface-dwelling rodent. *Behavioural Brain Research* **153**:389–395. DOI: https://doi.org/10.1016/j.bbr.2003.12.015, PMID: 15265634

Kimchi T, Reshef M, Terkel J. 2005. Evidence for the use of reflected self-generated seismic waves for spatial orientation in a blind subterranean mammal. *The Journal of Experimental Biology* **208**:647–659. DOI: https://doi.org/10.1242/jeb.01396, PMID: 15695757

Klauer G, Burda H, Nevo E. 1997. Adaptive differentiations of the skin of the head in a subterranean rodent, Spalax ehrenbergi. *Journal of Morphology* **233**:53–66. DOI: https://doi.org/10.1002/(SICI)1097-4687(199707)233:1<53::AID-JMOR5>3.0.CO;2-P, PMID: 9183854

Knotková E, Veitl S, Šumbera R, Sedláček F, Burda H. 2009. VOCALISATIONS OF THE SILVERY MOLE-RAT: COMPARISON OF VOCAL REPERTOIRES IN SUBTERRANEAN RODENTS WITH DIFFERENT SOCIAL SYSTEMS. *Bioacoustics* **18**:241–257. DOI: https://doi.org/10.1080/09524622.2009.9753604

Kompier NF, Keysers C, Gazzola V, Lucassen PJ, Krugers HJ. 2019. Early Life Adversity and Adult Social Behavior: Focus on Arginine Vasopressin and Oxytocin as Potential Mediators. *Frontiers in Behavioral Neuroscience* **13**:143. DOI: https://doi.org/10.3389/fnbeh.2019.00143, PMID: 31404254

Koob GF, Heinrichs SC, Menzaghi F, Pich EM, Britton KT. 1994. Corticotropin releasing factor, stress and behavior. *Seminars in Neuroscience* **6**:221–229. DOI: https://doi.org/10.1006/smns.1994.1029

Korn H, Taitt MJ. 1987. Initiation of early breeding in a population of Microtus townsendii (Rodentia) with the secondary plant compound 6-MBOA. *Oecologia* **71**:593–596. DOI: https://doi.org/10.1007/BF00379303, PMID: 28312233

Kriegsfeld LJ, Trasy AG, Nelson RJ. 2001. Temperature and Photoperiod Interact to Affect Reproduction and GnRH Synthesis in Male Prairie Voles. *Journal of Neuroendocrinology* **12**:553–558. DOI: https://doi.org/10.1046/j.1365-2826.2000.00485.x, PMID: 10844584

Lacey E, Patton J, Cameron G. 2001. Life Underground: The Biology Of Subterranean Rodents. *Australian Mammalogy* **23**:e75. DOI: https://doi.org/10.1071/AM01075_BR

Lange S, Neumann B, Hagemeyer P, Burda H. 2005. Kairomone-guided food location in subterranean Zambian mole-rats (Cryptomis spp., Bathyergidae. *Folia Zoologica-Praha* **54**:263–268.

Lee NS, Beery AK. 2019. Neural circuits underlying rodent sociality: a comparative approach. Lee NS (Ed). *Neuroendocrine Regulation of Behavior*. Springer. p. 211–238. DOI: https://doi.org/10.1007/978-3-030-38720-4

Lee KS, Dumke R, Paterek T. 2021. Numerical tests of magnetoreception models assisted with behavioral experiments on American cockroaches. *Scientific Reports* **11**:1–10. DOI: https://doi.org/10.1038/s41598-021-91815-x, PMID: 34108599

Leigh-Hunt N, Bagguley D, Bash K, Turner V, Turnbull S, Valtorta N, Caan W. 2017. An overview of systematic reviews on the public health consequences of social isolation and loneliness. *Public Health* **152**:157–171. DOI: https://doi.org/10.1016/j.puhe.2017.07.035, PMID: 28915435

Lim MM, Young LJ. 2006. Neuropeptidergic regulation of affiliative behavior and social bonding in animals. *Hormones and Behavior* **50**:506–517. DOI: https://doi.org/10.1016/j.yhbeh.2006.06.028

Lövy M, Šklíba J, Hrouzková E, Dvořáková V, Nevo E, Šumbera R, Reed AW. 2015. Habitat and Burrow System Characteristics of the Blind Mole Rat Spalax galili in an Area of Supposed Sympatric Speciation. *PLOS ONE* **10**:e0133157. DOI: https://doi.org/10.1371/journal.pone.0133157

Macdonald DW, Müller-Schwarze D, Natynczuk S. 1990. Chemical Signals in Vertebrates. Springer.

Malik A, Korol A, Hübner S, Hernandez AG, Thimmapuram J, Ali S, Glaser F, Paz A, Avivi A, Band M, Michalak P. 2011. Transcriptome Sequencing of the Blind Subterranean Mole Rat, Spalax galili: Utility and Potential for the Discovery of Novel Evolutionary Patterns. *PLOS ONE* **6**:e21227. DOI: https://doi.org/10.1371/journal.pone.0021227, PMID: 21857902

Mann MD, Rehkämper G, Reinke H, Frahm HD, Necker R, Nevo E. 1997. Size of somatosensory cortex and of somatosensory thalamic nuclei of the naturally blind mole rat, Spalax ehrenbergi. *Journal Fur Hirnforschung* **38**:47–59 PMID: 9059917.,

Manov I, Hirsh M, Iancu TC, Malik A, Sotnichenko N, Band M, Avivi A, Shams I. 2013. Pronounced cancer resistance in a subterranean rodent, the blind mole-rat, Spalax: in vivo and in vitroevidence. *BMC Biology* **11**:e91. DOI: https://doi.org/10.1186/1741-7007-11-91, PMID: 23937926

Marhold S, Wiltschko W, Burda H. 1997. A Magnetic Polarity Compass for Direction Finding in A Subterranean Mammal. *Naturwissenschaften* **84**:421–423. DOI: https://doi.org/10.1007/s001140050422

Martínez A, Arteaga-Silva M, Bonilla-Jaime H, Cárdenas M, Rojas-Castañeda J, Vigueras-Villaseñor R, Limón-Morales O, Luis J. 2019. Paternal behavior in the Mongolian gerbil, and its regulation by social factors, T, ERα, and AR. *Physiology & Behavior* **199**:351–358. DOI: https://doi.org/10.1016/j.physbeh.2018.12.001, PMID: 30529342

Mason MJ, Lai FWS, Li JG, Nevo E. 2010. Middle ear structure and bone conduction in Spalax, Eospalax, and Tachyoryctes mole-rats (Rodentia: Spalacidae. *Journal of Morphology* **271**:462–472. DOI: https://doi.org/10.1002/jmor.10810, PMID: 19941379

Matsumoto K, Pinna G, Puia G, Guidotti A, Costa E. 2005. Social isolation stress-induced aggression in mice: a model to study the pharmacology of neurosteroidogenesis. *Stress* **8**:85–93. DOI: https://doi.org/10.1080/10253890500159022, PMID: 16019600

Mazurek MO, Kanne SM, Wodka EL. 2013. Physical aggression in children and adolescents with autism spectrum disorders. *Research in Autism Spectrum Disorders* **7**:455–465. DOI: https://doi.org/10.1016/j.rasd.2012.11.004

McGraw LA, Young LJ. 2010. The prairie vole: an emerging model organism for understanding the social brain. *Trends in Neurosciences* **33**:103–109. DOI: https://doi.org/10.1016/j.tins.2009.11.006, PMID: 20005580

McGregor PK. 1997. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London. Series B* **340**:237–244. DOI: https://doi.org/10.1098/rstb.1993.0063

McIntyre AK. 1980. Biological seismography. *Trends in Neurosciences* **3**:202–205. DOI: https://doi.org/10.1016/0166-2236(80)90076-4

McNeal N, Scotti M-AL, Wardwell J, Chandler DL, Bates SL, Larocca M, Trahanas DM, Grippo AJ. 2014. Disruption of social bonds induces behavioral and physiological dysregulation in male and female prairie voles. *Autonomic Neuroscience* **180**:9–16. DOI: https://doi.org/10.1016/j.autneu.2013.10.001, PMID: 24161576

Mele A, Cabib S, Oliverio A, Melchiorri P, Puglisi-Allegra S. 1987. Effects of corticotropin releasing factor and sauvagine on social behavior of isolated mice. *Peptides* **8**:935–938. DOI: https://doi.org/10.1016/0196-9781(87)90083-0, PMID: 3501578

Merchenthaler I, Vigh S, Petrusz P, Schally AV. 1982. Immunocytochemical localization of corticotropin-releasing factor (CRF) in the rat brain. *The American Journal of Anatomy* **165**:385–396. DOI: https://doi.org/10.1002/aja.1001650404, PMID: 6760710

Moolman M, Bennett NC, Schoeman AS. 2006. The social structure and dominance hierarchy of the highveld mole-rat Cryptomys hottentotus pretoriae (Rodentia: Bathyergidae). *Journal of Zoology* **246**:193–201. DOI: https://doi.org/10.1111/j.1469-7998.1998.tb00148.x

Mooney SJ, Holmes MM. 2013. Social condition and oxytocin neuron number in the hypothalamus of naked mole-rats (Heterocephalus glaber). *Neuroscience* **230**:56–61. DOI: https://doi.org/10.1016/j.neuroscience.2012.11.014, PMID: 23200787

Mooney SJ, Douglas NR, Holmes MM. 2014. Peripheral administration of oxytocin increases social affiliation in the naked mole-rat (Heterocephalus glaber). *Hormones and Behavior* **65**:380–385. DOI: https://doi.org/10.1016/j.yhbeh.2014.02.003, PMID: 24530845

Moore RY, Speh JC, Card JP. 1995. The retinohypothalamic tract originates from a distinct subset of retinal ganglion cells. *The Journal of Comparative Neurology* **352**:351–366. DOI: https://doi.org/10.1002/cne.903520304, PMID: 7706557

Mortimer B. 2017. Biotremology: Do physical constraints limit the propagation of vibrational information? *Animal Behaviour* **130**:165–174. DOI: https://doi.org/10.1016/j.anbehav.2017.06.015

Müller M, Burda H. 1989. Restricted hearing range in a subterranean rodent, Cryptomys hottentotus. *Die Naturwissenschaften* **76**:134–135. DOI: https://doi.org/10.1007/BF00366611, PMID: 2725692

Mumtaz F, Khan MI, Zubair M, Dehpour AR. 2018. Neurobiology and consequences of social isolation stress in animal model-A comprehensive review. *Biomedicine & Pharmacotherapy = Biomedecine & Pharmacotherapie* **105**:1205–1222. DOI: https://doi.org/10.1016/j.biopha.2018.05.086, PMID: 30021357

Nakane Y, Yoshimura T. 2014. Universality and diversity in the signal transduction pathway that regulates seasonal reproduction in vertebrates. *Frontiers in Neuroscience* **8**:115. DOI: https://doi.org/10.3389/fnins.2014.00115, PMID: 24959116

Narins PM, Reichman OJ, Jarvis JU, Lewis ER. 1992. Seismic signal transmission between burrows of the Cape mole-rat, Georychus capensis. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology* **170**:13–21. DOI: https://doi.org/10.1007/BF00190397, PMID: 1573567

Narins PM, Lewis ER, Jarvis JJ, O'Riain J. 1997. The use of seismic signals by fossorial southern African mammals: a neuroethological gold mine. *Brain Research Bulletin* **44**:641–646. DOI: https://doi.org/10.1016/s0361-9230(97)00286-4, PMID: 9365810

Narins P, Losin N, O'Connell-Rodwell C. 2009. Encyclopedia of Neuroscience. Springer. DOI: https://doi.org/10.1007/978-3-540-29678-2

Necker R, Rehkämper G, Nevo E. 1992. Electrophysiological mapping of body representation in the cortex of the blind mole rat. *NeuroReport* **3**:505–508. DOI: https://doi.org/10.1097/00001756-199206000-00012

Nei M, Niimura Y, Nozawa M. 2008. The evolution of animal chemosensory receptor gene repertoires: roles of chance and necessity. *Nature Reviews. Genetics* **9**:951–963. DOI: https://doi.org/10.1038/nrg2480, PMID: 19002141

Nevo E. 1961. Observations on Israeli populations of the mole rat spalax E. Ehrenbergi Nehring 1898. *Mammalia* **25**:127–144. DOI: https://doi.org/10.1515/mamm.1961.25.2.127

Nevo E. 1969. Mole rat spalax ehrenbergi: mating behavior and its evolutionary significance. *Science* **163**:484–486. DOI: https://doi.org/10.1126/science.163.3866.484, PMID: 5762401

Nevo E, Naftali G, Guttman R. 1975. Aggression patterns and speciation. *PNAS* **72**:3250–3254. DOI: https://doi.org/10.1073/pnas.72.8.3250, PMID: 1059109

Nevo E, Bodmer M, Heth G. 1976. Olfactory discrimination as an isolating mechanism in speciating mole rats. *Experientia* **32**:1511–1512. DOI: https://doi.org/10.1007/BF01924423, PMID: 1035542

Nevo E. 1979. Adaptive Convergence and Divergence of Subterranean Mammals. *Annual Review of Ecology and Systematics* **10**:269–308. DOI: https://doi.org/10.1146/annurev.es.10.110179.001413

Nevo E, Heth G, Beiles A. 1982. Population structure and evolution in subterranean mole rats. *Evolution; International Journal of Organic Evolution* **36**:1283–1289. DOI: https://doi.org/10.1111/j.1558-5646.1982.tb05497.x, PMID: 28563553

Nevo E. 1985. Speciation in action and adaptation in subterranean mole rats: patterns and theory. *Bolletino Di Zoologia* **52**:65–95. DOI: https://doi.org/10.1080/11250008509440344

Nevo E, Heth G, Beiles A. 1986. Aggression patterns in adaptation and speciation of subterranean mole rats. *Journal of Genetics* **65**:65–78. DOI: https://doi.org/10.1007/BF02923537

Nevo E, Heth G, Beiles A, Frankenberg E. 1987. Geographic dialects in blind mole rats: role of vocal communication in active speciation. *PNAS* **84**:3312–3315. DOI: https://doi.org/10.1073/pnas.84.10.3312, PMID: 3472211

Nevo E, Heth G, Pratt H. 1991. Seismic communication in a blind subterranean mammal: a major somatosensory mechanism in adaptive evolution underground. *PNAS* **88**:1256–1260. DOI: https://doi.org/10.1073/pnas.88.4.1256, PMID: 1996326

Nevo E. 1999. Mosaic Evolution of Subterranean Mammals. Regression, Progression and Global Convergence. Oxford, UK: Oxford University Press. DOI: https://doi.org/10.1007/978-3-540-69276-8_28

Nevo E. 2013. Stress, adaptation, and speciation in the evolution of the blind mole rat, Spalax, in Israel. *Molecular Phylogenetics and Evolution* **66**:515–525. DOI: https://doi.org/10.1016/j.ympev.2012.09.008, PMID: 23032572

Okhovat M, Berrio A, Wallace G, Ophir AG, Phelps SM. 2015. Sexual fidelity trade-offs promote regulatory variation in the prairie vole brain. *Science* **350**:1371–1374. DOI: https://doi.org/10.1126/science.aac5791, PMID: 26659055

Oliveira V, Lukas M, Wolf HN, Durante E, Lorenz A, Mayer AL, Bludau A, Bosch OJ, Grinevich V, Egger V, de Jong TR, Neumann ID. 2021. Oxytocin and vasopressin within the ventral and dorsal lateral septum modulate aggression in female rats. *Nature Communications* **12**:1–15. DOI: https://doi.org/10.1038/s41467-021-23064-5, PMID: 34006875

Oster H, Avivi A, Joel A, Albrecht U, Nevo E. 2002. A Switch from Diurnal to Nocturnal Activity in S. ehrenbergi Is Accompanied by an Uncoupling of Light Input and the Circadian Clock. *Current Biology* **12**:1919–1922. DOI: https://doi.org/10.1016/S0960-9822(02)01263-0

O'Connell LA, Hofmann HA. 2011. Genes, hormones, and circuits: An integrative approach to study the evolution of social behavior. *Frontiers in Neuroendocrinology* **32**:320–335. DOI: https://doi.org/10.1016/j.yfrne.2010.12.004

Park TJ, Catania KC, Samaan D, Comer CM. 2007. Adaptive neural organization of naked mole-rat somatosensation (and those similarly challenged). Begall S, Burda H, Schleich CE (Eds). *Subterranean Rodents*. Springer. p. 175–193. DOI: https://doi.org/10.1007/978-3-540-69276-8_13

Pevet P, Heth G, Hiam A, Nevo E. 1984. Photoperiod perception in the blind mole rat (Spalax ehrenbergi, Nehring): Involvement of the Harderian gland, atrophied eyes, and melatonin. *Journal of Experimental Zoology* **232**:41–50. DOI: https://doi.org/10.1002/jez.1402320106

Phillips JB, Borland SC. 1992. Behavioural evidence for use of a light-dependent magnetoreception mechanism by a vertebrate. *Nature* **359**:142–144. DOI: https://doi.org/10.1038/359142a0

Pietrabissa G, Simpson SG. 2020. Psychological Consequences of Social Isolation During COVID-19 Outbreak. *Frontiers in Psychology* **11**:2201. DOI: https://doi.org/10.3389/fpsyg.2020.02201, PMID: 33013572

Prosen CA, Petersen MR, Moody DB, Stebbins WC. 1978. Auditory thresholds and kanamycin-induced hearing loss in the guinea pig assessed by a positive reinforcement procedure. *The Journal of the Acoustical Society of America* **63**:559–566. DOI: https://doi.org/10.1121/1.381754, PMID: 670552

Prounis GS, Ophir AG. 2020. One cranium, two brains not yet introduced: Distinct but complementary views of the social brain. *Neuroscience and Biobehavioral Reviews* **108**:231–245. DOI: https://doi.org/10.1016/j.neubiorev.2019.11.011, PMID: 31743724

Prox L, Farine D. 2020. A framework for conceptualizing dimensions of social organization in mammals. *Ecology and Evolution* **10**:791–807. DOI: https://doi.org/10.1002/ece3.5936, PMID: 32015844

Prsa M, Morandell K, Cuenu G, Huber D. 2019. Feature-selective encoding of substrate vibrations in the forelimb somatosensory cortex. *Nature* **567**:384–388. DOI: https://doi.org/10.1038/s41586-019-1015-8, PMID: 30867600

Prsa M, Kilicel D, Nourizonoz A, Lee KS, Huber D. 2021. A common computational principle for vibrotactile pitch perception in mouse and human. *Nature Communications* **12**:1–8. DOI: https://doi.org/10.1038/s41467-021-25476-9, PMID: 34504074

Qiao X, Yan Y, Wu R, Tai F, Hao P, Cao Y, Wang J. 2013. Sociality and oxytocin and vasopressin in the brain of male and female dominant and subordinate mandarin voles. *Journal of Comparative Physiology A* **200**:149–159. DOI: https://doi.org/10.1007/s00359-013-0870-2

Rado R, Levi N, Hauser H, Witcher J, Alder N, Intrator N, Wollberg Z, Terkel J. 1987. Seismic signalling as a means of communication in a subterranean mammal. *Animal Behaviour* **35**:1249–1251. DOI: https://doi.org/10.1016/S0003-3472(87)80183-5

Rado R, Himelfarb M, Arensburg B, Terkel J, Wollberg Z. 1989. Are seismic communication signals transmitted by bone conduction in the blind mole rat? *Hearing Research* **41**:23–29. DOI: https://doi.org/10.1016/0378-5955(89)90175-5, PMID: 2793611

Rado R, Gev H, Goldman B, Terkel J. 1991a. Light and Circadian Activity in the Blind Mole Rat In Photobiology. Riklis E (Ed). *Photobiology*. Boston, MA: Springer. p. 581–589. DOI: https://doi.org/10.1007/978-1-4615-3732-8_61

Rado R, Wollberg Z, Terkel J. 1991b. The ontogeny of seismic communication during dispersal in the blind mole rat. *Animal Behaviour* **42**:15–21. DOI: https://doi.org/10.1016/S0003-3472(05)80601-3

Rado R, Bronchti G, Wollberg Z, Terkel J. 1992. Sensitivity to Light of the Blind Mole Rat - Behavioral and Neuroanatomical Study. *Israel J Zool* **38**:323–331.

Rado R, Shanas U, Zuri I, Terkel J. 1993. Seasonal Activity in the Blind Mole-Rat (Spalax-Ehrenbergi. *Canadian Journal of Zoology* **71**:1733–1737. DOI: https://doi.org/10.1139/z93-245

Rado R, Terkel J, Wollberg Z. 1998. Seismic communication signals in the blind mole-rat (Spalax ehrenbergi): electrophysiological and behavioral evidence for their processing by the auditory system. *Journal of Comparative Physiology A* **183**:503–511. DOI: https://doi.org/10.1007/s003590050275, PMID: 9809454

Randall JA, Lewis ER. 1997. Seismic communication between the burrows of kangaroo rats, Dipodomys spectabilis. *Journal of Comparative Physiology. A, Sensory, Neural, and Behavioral Physiology* **181**:525–531. DOI: https://doi.org/10.1007/s003590050136, PMID: 9373957

Randall JA. 2013. Vibrational Communication: Spiders to Kangaroo Rats In Biocommunication of Animals. Witzany G (Ed). *Biocommunication of Animals*. Springer. p. 103–133. DOI: https://doi.org/10.1007/978-94-007-7414-8

Rauschecker JP, Kniepert U. 1994. Auditory Localization Behaviour in Visually Deprived Cats. *European Journal of Neuroscience* **6**:149–160. DOI: https://doi.org/10.1111/j.1460-9568.1994.tb00256.x

Rehkämper G, Necker R, Nevo E. 1994. Functional anatomy of the thalamus in the blind mole rat *Spalax ehrenbergi* : An architectonic and electrophysiologically controlled tracing study . *Journal of Comparative Neurology* **347**:570–584. DOI: https://doi.org/10.1002/cne.903470408

Remage-Healey L, Krentzel AA, Macedo-Lima M, Vahaba D. 2017. Species Diversity Matters in Biological Research. *Policy Insights from the Behavioral and Brain Sciences* **4**:210–218. DOI: https://doi.org/10.1177/2372732217719908

Resendez SL, Namboodiri VMK, Otis JM, Eckman LEH, Rodriguez-Romaguera J, Ung RL, Basiri ML, Kosyk O, Rossi MA, Dichter GS, Stuber GD. 2020. Social Stimuli Induce Activation of Oxytocin Neurons Within the Paraventricular Nucleus of the Hypothalamus to Promote Social Behavior in Male Mice. *The Journal of Neuroscience* **40**:2282–2295. DOI: https://doi.org/10.1523/JNEUROSCI.1515-18.2020, PMID: 32024781

Richter TA, Malpaux B, Fleming PA, Molteno AJ, Bennett NC. 2006. Melatonin secretion in a strictly subterranean mammal, the Damaraland mole-rat (*Cryptomys damarensis*). *Journal of Zoology* **261**:313–319. DOI: https://doi.org/10.1017/S0952836903004254

Roberts WA. 2006. Animal Memory: Episodic-like Memory in Rats. *Current Biology* **16**:R601–R603. DOI: https://doi.org/10.1016/j.cub.2006.07.001, PMID: 16890521

Rosen GJ, de Vries GJ, Goldman SL, Goldman BD, Forger NG. 2008. Distribution of oxytocin in the brain of a eusocial rodent. *Neuroscience* **155**:809–817. DOI: https://doi.org/10.1016/j.neuroscience.2008.05.039, PMID: 18582538

Roy C, Lagarde J, Dotov D, Dalla Bella S. 2017. Walking to a multisensory beat. *Brain and Cognition* **113**:172–183. DOI: https://doi.org/10.1016/j.bandc.2017.02.002, PMID: 28257971

Sadka RS, Wollberg Z. 2004. Response properties of auditory activated cells in the occipital cortex of the blind mole rat: an electrophysiological study. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* **190**:403–413. DOI: https://doi.org/10.1007/s00359-004-0506-7, PMID: 15029448

Sanchez-Andrade G, Kendrick KM. 2009. The main olfactory system and social learning in mammals. *Behavioural Brain Research* **200**:323–335. DOI: https://doi.org/10.1016/j.bbr.2008.12.021, PMID: 19150375

Schadler MH, Butterstein GM, Faulkner BJ, Rice SC, Weisinger LA. 1988. The plant metabolite, 6-methoxybenzoxazolinone, stimulates an increase in secretion of follicle-stimulating hormone and size of reproductive organs in Microtus pinetorum. *Biology of Reproduction* **38**:817–820. DOI: https://doi.org/10.1095/biolreprod38.4.817, PMID: 3135852

Schmidt H, Malik A, Bicker A, Poetzsch G, Avivi A, Shams I, Hankeln T. 2017. Hypoxia tolerance, longevity and cancer-resistance in the mole rat Spalax - a liver transcriptomics approach. *Scientific Reports* **7**:14348. DOI: https://doi.org/10.1038/s41598-017-13905-z, PMID: 29084988

Scott N, Prigge M, Yizhar O, Kimchi T. 2015. A sexually dimorphic hypothalamic circuit controls maternal care and oxytocin secretion. *Nature* **525**:519–522. DOI: https://doi.org/10.1038/nature15378, PMID: 26375004

Seyfarth RM, Cheney DL. 2003. Meaning and emotion in animal vocalizations. *Annals of the New York Academy of Sciences* **1000**:32–55. DOI: https://doi.org/10.1196/annals.1280.004, PMID: 14766619

Shabalova AA, Liang M, Zhong J, Huang Z, Tsuji C, Shnayder NA, Lopatina O, Salmina AB, Okamoto H, Yamamoto Y, Zhong ZG, Yokoyama S, Higashida H. 2020. Oxytocin and CD38 in the paraventricular nucleus play a critical role in paternal aggression in mice. *Hormones and Behavior* **120**:e104695. DOI: https://doi.org/10.1016/j.yhbeh.2020.104695, PMID: 31987898

Shams I, Avivi A, Nevo E. 2005. Oxygen and carbon dioxide fluctuations in burrows of subterranean blind mole rats indicate tolerance to hypoxic–hypercapnic stresses. *Comparative Biochemistry and Physiology Part A* **142**:376–382. DOI: https://doi.org/10.1016/j.cbpa.2005.09.003, PMID: 16223592

Shanas U, Heth G, Nevo E, Shalgi R, Terkel J. 1995. Reproductive-Behavior in the Female Blind Mole-Rat (Spalax-Ehrenbergi. *Journal of Zoology* **237**:195–210. DOI: https://doi.org/10.1111/j.1469-7998.1995.tb02758.x

Shanas U, Terkel J. 1995. Grooming expresses harderian gland materials in the blind mole rat. *Aggressive Behavior* **21**:137–146. DOI: https://doi.org/10.1002/1098-2337(1995)21:2<137::AID-AB2480210206>3.0.CO;2-Z

Shanas U, Terkel J. 1997. Mole-rat harderian gland secretions inhibit aggression. *Animal Behaviour* **54**:1255–1263. DOI: https://doi.org/10.1006/anbe.1997.0533, PMID: 9398378

Shanas U, Terkel J. 1999. The Harderian Gland of the Blind Mole Rat. Shanas U (Ed). *Advances in Chemical Signals in Vertebrates*. Boston, MA: Springer. p. 343–358. DOI: https://doi.org/10.1007/978-1-4615-4733-4

Shemesh Y, Sztainberg Y, Forkosh O, Shlapobersky T, Chen A, Schneidman E. 2013. High-order social interactions in groups of mice. *eLife* **2**:e00759. DOI: https://doi.org/10.7554/eLife.00759, PMID: 24015357

Shi P, Zhang J. 2007. Comparative genomic analysis identifies an evolutionary shift of vomeronasal receptor gene repertoires in the vertebrate transition from water to land. *Genome Research* **17**:166–174. DOI: https://doi.org/10.1101/gr.6040007, PMID: 17210926

Silverman RT, Munger BL, Halata Z. 1986. The sensory innervation of the rat rhinarium. *The Anatomical Record* **214**:210–225. DOI: https://doi.org/10.1002/ar.1092140217, PMID: 3954078

Smith CC, Reichman OJ. 1984. The Evolution of Food Caching by Birds and Mammals. *Annual Review of Ecology and Systematics* **15**:329–351. DOI: https://doi.org/10.1146/annurev.es.15.110184.001553

Smith TD, Bhatnagar KP, Dennis JC, Morrison EE, Park TJ. 2007. Growth-deficient vomeronasal organs in the naked mole-rat (Heterocephalus glaber. *Brain Research* **1132**:78–83. DOI: https://doi.org/10.1016/j.brainres.2006.11.021, PMID: 17188655

Sofroniew MV, Weindl A, Schinko I, Wetzstein R. 1979. The distribution of vasopressin-, oxytocin-, and neurophysin-producing neurons in the guinea pig brain. *Cell and Tissue Research* **196**:367–384. DOI: https://doi.org/10.1007/BF00234734, PMID: 378381

Swearer JM, Drachman DA, O'Donnell BF, Mitchell AL. 1988. Troublesome and disruptive behaviors in dementia. Relationships to diagnosis and disease severity. *Journal of the American Geriatrics Society* **36**:784–790. DOI: https://doi.org/10.1111/j.1532-5415.1988.tb04260.x, PMID: 3411060

Taheri Zadeh Z, Rahmani S, Alidadi F, Joushi S, Esmaeilpour K. 2021. Depresssion, anxiety and other cognitive consequences of social isolation: Drug and non-drug treatments. *International Journal of Clinical Practice* **75**:e14949. DOI: https://doi.org/10.1111/ijcp.14949, PMID: 34614276

Takayanagi Y, Yoshida M, Bielsky IF, Ross HE, Kawamata M, Onaka T, Yanagisawa T, Kimura T, Matzuk MM, Young LJ, Nishimori K. 2005. Pervasive social deficits, but normal parturition, in oxytocin receptor-deficient mice. PNAS **102**:16096–16101. DOI: https://doi.org/10.1073/pnas.0505312102, PMID: 16249339

Tan O, Musullulu H, Raymond JS, Wilson B, Langguth M, Bowen MT. 2019. Oxytocin and vasopressin inhibit hyper-aggressive behaviour in socially isolated mice. *Neuropharmacology* **156**:107573. DOI: https://doi.org/10.1016/j.neuropharm.2019.03.016, PMID: 30885607

Tibbetts EA, Dale J. 2007. Individual recognition: it is good to be different. *Trends in Ecology & Evolution* **22**:529–537. DOI: https://doi.org/10.1016/j.tree.2007.09.001, PMID: 17904686

Toldi J, Farkas T, Völgyi B. 1994a. Neonatal enucleation induces cross-modal changes in the barrel cortex of rat. A behavioural and electrophysiological study. *Neuroscience Letters* **167**:1–4. DOI: https://doi.org/10.1016/0304-3940(94)91014-6, PMID: 8177504

Toldi J, Rojik I, Fehér O. 1994b. Neonatal monocular enucleation-induced cross-modal effects observed in the cortex of adult rat. *Neuroscience* **62**:105–114. DOI: https://doi.org/10.1016/0306-4522(94)90318-2, PMID: 7816193

Tsuda MC, Yamaguchi N, Ogawa S. 2011. Early life stress disrupts peripubertal development of aggression in male mice. *Neuroreport* **22**:259–263. DOI: https://doi.org/10.1097/WNR.0b013e328344495a, PMID: 21403582

Valesky EM, Burda H, Kaufmann R, Oelschläger HHA. 2012. Distribution of oxytocin- and vasopressin-immunoreactive neurons in the brain of the eusocial mole rat (Fukomys anselli). *Anatomical Record* **295**:474–480. DOI: https://doi.org/10.1002/ar.22414, PMID: 22266748

Veenema AH, Blume A, Niederle D, Buwalda B, Neumann ID. 2006. Effects of early life stress on adult male aggression and hypothalamic vasopressin and serotonin. *The European Journal of Neuroscience* **24**:1711–1720. DOI: https://doi.org/10.1111/j.1460-9568.2006.05045.x, PMID: 17004935

Veenema AH, Bredewold R, Neumann ID. 2007. Opposite effects of maternal separation on intermale and maternal aggression in C57BL/6 mice: link to hypothalamic vasopressin and oxytocin immunoreactivity. *Psychoneuroendocrinology* **32**:437–450. DOI: https://doi.org/10.1016/j.psyneuen.2007.02.008, PMID: 17433558

Veenema AH, Neumann ID. 2008. Central vasopressin and oxytocin release: regulation of complex social behaviours. *Progress in Brain Research* **170**:261–276. DOI: https://doi.org/10.1016/S0079-6123(08)00422-6, PMID: 18655888

Veenema AH, Neumann ID. 2009. Maternal separation enhances offensive play-fighting, basal corticosterone and hypothalamic vasopressin mRNA expression in juvenile male rats. *Psychoneuroendocrinology* **34**:463–467. DOI: https://doi.org/10.1016/j.psyneuen.2008.10.017, PMID: 19056182

Vleck D. 1979. The Energy Cost of Burrowing by the Pocket Gopher Thomomys bottae. *Physiological Zoology* **52**:122–136. DOI: https://doi.org/10.1086/physzool.52.2.30152558

Vuillez P, Herbin M, Cooper HM, Nevo E, Pévet P. 1994. Photic induction of Fos immunoreactivity in the suprachiasmatic nuclei of the blind mole rat (Spalax ehrenbergi). *Brain Research* **654**:81–84. DOI: https://doi.org/10.1016/0006-8993(94)91573-3, PMID: 7526965

Wei B, Tai F, Liu X, Ma L, Yang X, Jia R, Zhang X. 2013. Neonatal tactile stimulation alleviates the negative effects of neonatal isolation on novel object recognition, sociability and neuroendocrine levels in male adult mandarin voles (Microtus mandarinus). *Physiology & Behavior* **112–113**:14–22. DOI: https://doi.org/10.1016/j.physbeh.2013.02.005, PMID: 23438372

Wiltschko W, Wiltschko R. 1982. The role of outward journey information in the orientation of homing pigeons. Wiltschko W (Ed). *Avian Navigation*. Springer. p. 239–252. DOI: https://doi.org/10.1007/978-3-642-68616-0

Wiltschko W, Munro U, Ford H, Wiltschko R. 1993. Red light disrupts magnetic orientation of migratory birds. *Nature* **364**:525–527. DOI: https://doi.org/10.1038/364525a0

Wiltschko R, Munro U, Ford H, Stapput K, Wiltschko W. 2008. Light-dependent magnetoreception: orientation behaviour of migratory birds under dim red light. *The Journal of Experimental Biology* **211**:3344–3350. DOI: https://doi.org/10.1242/jeb.020313, PMID: 18840669

Winslow JT, Hearn EF, Ferguson J, Young LJ, Matzuk MM, Insel TR. 2000. Infant Vocalization, Adult Aggression, and Fear Behavior of an Oxytocin Null Mutant Mouse. *Hormones and Behavior* **37**:145–155. DOI: https://doi.org/10.1006/hbeh.1999.1566, PMID: 10753584

Xu L, Pan Y, Young KA, Wang Z, Zhang Z. 2010. Oxytocin and vasopressin immunoreactive staining in the brains of Brandt's voles (Lasiopodomys brandtii) and greater long-tailed hamsters (Tscherskia triton). *Neuroscience* **169**:1235–1247. DOI: https://doi.org/10.1016/j.neuroscience.2010.05.064, PMID: 20573572

Yaka R, Yinon U, Rosner M, Wollberg Z. 2000. Pathological and experimentally induced blindness induces auditory activity in the cat primary visual cortex. *Experimental Brain Research* **131**:144–148. DOI: https://doi.org/10.1007/s002219900295, PMID: 10759180

Yamamoto Y, Cushing BS, Kramer KM, Epperson PD, Hoffman GE, Carter CS. 2004. Neonatal manipulations of oxytocin alter expression of oxytocin and vasopressin immunoreactive cells in the paraventricular nucleus of the hypothalamus in a gender-specific manner. *Neuroscience* **125**:947–955. DOI: https://doi.org/10.1016/j.neuroscience.2004.02.028, PMID: 15120854

Yartsev MM. 2017. The emperor's new wardrobe: Rebalancing diversity of animal models in neuroscience research. *Science* **358**:466–469. DOI: https://doi.org/10.1126/science.aan8865, PMID: 29074765

Yi X, Yi S, Deng Y, Wang M, Ju M. 2021. High-valued seeds are remembered better: evidence for item-based spatial memory of scatter-hoarding rodents. *Animal Behaviour* **175**:1–6. DOI: https://doi.org/10.1016/j.anbehav.2021.02.009

Yoerg SI. 1999. Solitary is not Asocial: Effects of Social Contact in Kangaroo Rats (Heteromyidae: Dipodomys heermanni). *Ethology: Formerly Zeitschrift Fur Tierpsychologie* **105**:317–333. DOI: https://doi.org/10.1046/j.1439-0310.1999.00392.x

Yohn CN, Leithead AB, Becker EA. 2017. Increased vasopressin expression in the BNST accompanies paternally induced territoriality in male and female California mouse offspring. *Hormones and Behavior* **93**:9–17. DOI: https://doi.org/10.1016/j.yhbeh.2017.03.008

Yoshimura T. 2013. Thyroid hormone and seasonal regulation of reproduction. *Frontiers in Neuroendocrinology* **34**:157–166. DOI: https://doi.org/10.1016/j.yfrne.2013.04.002

Zenuto RR, Vassallo AI, Busch C. 2001. A method for studying social and reproductive behaviour of subterranean rodents in captivity. *Acta Theriologica* **46**:161–170. DOI: https://doi.org/10.4098/AT.arch.01-18

Zhao H. 2021. Evolution of V1R Repertoires in Subterranean Rodents. *Molecular Biology and Evolution* **32**:835–845. DOI: https://doi.org/10.1002/047001590X

Zilkha N, Sofer Y, Beny Y, Kimchi T. 2016. From classic ethology to modern neuroethology: overcoming the three biases in social behavior research. *Current Opinion in Neurobiology* **38**:96–108. DOI: https://doi.org/10.1016/j.conb.2016.04.014

Zilkha N, Sofer Y, Kashash Y, Kimchi T. 2021. The social network: Neural control of sex differences in reproductive behaviors, motivation, and response to social isolation. *Current Opinion in Neurobiology* **68**:137–151. DOI: https://doi.org/10.1016/j.conb.2021.03.005, PMID: 33910083

Zuri I, Terkel J. 1996. Locomotor patterns, territory, and tunnel utilization in the mole-rat Spalax ehrenbergi. *Journal of Zoology* **240**:123–140. DOI: https://doi.org/10.1111/j.1469-7998.1996.tb05490.x

Zuri I, Terkel J. 1998. Ontogeny of agonistic behaviour in dispersing blind mole rats (*spalax ehrenbergi*). *Aggressive Behavior* **24**:455–470. DOI: https://doi.org/10.1002/(SICI)1098-2337(1998)24:6<455::AID-AB5>3.0.CO;2-L

Zuri I, Fishelson L, Terkel J. 1998a. Morphology and cytology of the nasal cavity and vomeronasal organ in juvenile and adult blind mole rats (Spalax ehrenbergi. *The Anatomical Record* **251**:460–471. DOI: https://doi.org/10.1002/(SICI)1097-0185(199808)251:4<460::AID-AR5>3.0.CO;2-W

Zuri I, Gottreich A, Terkel J. 1998b. Social stress in neighboring and encountering blind mole-rats (Spalax ehrenbergi. *Physiology & Behavior* **64**:611–620. DOI: https://doi.org/10.1016/S0031-9384(98)00085-7