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RESEARCH ARTICLE

Evoked auditory potentials from African mole-rats and coruros reveal disparity in subterranean rodent hearing

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ABSTRACT

Hearing in subterranean rodents exhibits numerous peculiarities, including low sensitivity and restriction to a narrow range of comparatively low frequencies. Past studies provided two conflicting hypotheses explaining how these derived traits evolved: structural degeneration and adaptive specialization. To further elucidate this issue, we recorded auditory brainstem responses from three species of social subterranean rodents that differ in the degree of specialization to the underground habitat: the naked mole-rat (*Heterocephalus glaber*) and the Mashona mole-rat (*Fukomys darlingi*), which represent the ancient lineage of African mole-rats (Bathyergidae), and the coruro (*Spalacopus cyanus*), a South American rodent (Octodontidae) that adopted a subterranean lifestyle in more recent geological time. Additionally, we measured call amplitudes of social vocalizations to study auditory vocal coupling. We found elevated auditory thresholds and severe hearing range restrictions in the African mole-rats, with hearing in naked mole-rats tending to be more sensitive than in Mashona mole-rats, in which hearing notably deteriorated with increasing age. In contrast, hearing in coruros was similar to that of epigeic rodents, with its range extending into ultrasonic frequencies. However, as in the mole-rats, the coruros' region of best hearing was located at low frequencies close to 1 kHz. We argue that the auditory sensitivity of African mole-rats, although remarkably poor, has been underestimated by recent studies, whereas data on coruros conform to previous results. Considering the available evidence, we propose to be open to both degenerative and adaptive interpretations of hearing physiology in subterranean mammals, as each may provide convincing explanations for specific auditory traits observed.

KEY WORDS: Auditory brainstem response, Auditory threshold, Call amplitude, Naked mole-rat, Common mole-rat, *Spalacopus cyanus*

INTRODUCTION

Rodents have adopted subterranean lifestyles numerous times, with approximately 250 extant species from six families living predominately underground in self-maintained burrows (Begall et al., 2007). The subterranean realm poses several challenges to sensory physiology that must be overcome to meet the communicative and navigational demands of the animals. Although such limitations might be particularly obvious for visual communication, they are also relevant for hearing underground. The tunnel acoustics of the underground habitat differ in several aspects from surface conditions. Besides the obvious constraints of long-range and directional acoustic signaling within a burrow system, the subterranean realm is characterized by marked frequency-dependent differences in sound transmission. Frequencies higher than 1 kHz are notably attenuated, even over distances of just a few meters, while lower frequencies might be amplified (Heth et al., 1986; Lange et al., 2007; Okanoya et al., 2018). For instance, frequencies ranging between 200 and 800 Hz can experience a more than twofold sound pressure amplification in natural burrow systems of African mole-rats that live in tunnels varying between 4.5 and 9 cm in diameter (Lange et al., 2007). This phenomenon has been termed the stethoscope effect.

Facing these circumstances, subterranean rodents have adopted different strategies to communicate effectively underground. Most lineages are predominately represented by solitary burrowers, and few species (most of them within the African mole-rat family Bathyergidae and the mole-vole genus *Ellobius*) form social groups of varying size and complexity (Smorkatcheva and Kumaitova, 2014). Solitary species of several burrowing rodent taxa communicate with conspecifics in neighboring tunnels via seismic signals that are picked up by the somatosensory system, such as foot drumming (Narins et al., 1992) and head thumping (Hrouzková et al., 2018). However, this behavior is not known from social taxa. The latter communicate exclusively with conspecifics that they share a burrow system with and rely heavily on frequently exchanged vocal signals for that matter (Schleich et al., 2007; Bednářová et al., 2013; Barker et al., 2021). Both solitary and social species have evolved to exploit tunnel acoustics by shifting the pitch of their vocalizations into lower frequency ranges than what would be expected for rodents of their body size, often below 1 kHz (Capranica et al., 1974; Credner et al., 1997; Schleich and Busch, 2002; Devries and Sikes, 2008; but see Volodin et al., 2021).

The peculiar acoustic properties of their habitat in conjunction with the demands of social communication have created prolonged interest in the hearing capabilities of subterranean rodents. Two main trajectories have been proposed to characterize the evolution of hearing in these animals: degeneration and adaptive specialization (Burda et al., 1992; Burda, 2006). The degeneration hypothesis was popularized by Heffner and Heffner (1990, 1992, 1993), but it had already been foreshadowed by Fleischer (1973) in his morphological investigations. Heffner and Heffner (1990, 1992, 1993) employed a conditioned avoidance method to generate behavioral audiograms of their study species. They discovered unusually high auditory thresholds and narrow ranges of audible frequencies in subterranean rodent taxa compared with epigeic groups, as well as a consistent loss of the ability to localize short sound bursts. Although it was noted that all subterranean species displayed their greatest hearing sensitivity in the range of low-pitched sounds between 1 and 4 kHz, it was also pointed out that the respective thresholds at these

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frequencies were not lower than in surface-dwelling mammals (Heffner and Masterton, 1980; Heffner and Heffner, 1992). Analogous to the reduction of the visual system in animals living in light-deprived environments, Heffner and Heffner (1990) proposed that the subterranean realm would permit a degeneration of hearing by the absence of selective pressures maintaining it.

Contrary to this notion, other researchers put forward an adaptive interpretation of the patterns observed (Bruns et al., 1988; Burda et al., 1992). Proponents of this school diagnosed the lack of pinnae, the narrow and typically cerumen-filled auditory meatus, and the low efficiency of sound propagation in the middle ear as causes for the poor hearing sensitivity of subterranean mammals. However, these and other alterations of the ear in burrowing species do not necessarily represent degenerate traits (Burda et al., 1992). Respective authors have emphasized the low high-frequency cut-off as a stable and defining trait of subterranean rodent audiograms, non-randomly maintaining sensitivity to low-pitched, ecologically relevant frequencies. The overall reduction of hearing sensitivity was also interpreted to serve an adaptive purpose by countering the stethoscope effect and thereby preventing overstimulation of the ear during social encounters (Burda et al., 1992; Lange et al., 2007). Most studies on subterranean rodent hearing have since adopted the specialization hypothesis (Burda, 2006; Gessele et al., 2016) but arguments for hearing degeneration continue to be made (Mason et al., 2016).

Recently, Pyott et al. (2020) revived the discussion by presenting a comprehensive set of electrophysiological, molecular, and morphological data that could provide functional explanations for poor hearing in the two most intensively studied social subterranean rodent genera: *Heterocephalus* (naked mole-rats) and *Fukomys* (Northern common mole-rats). The authors argue that the functionality of the cochlear amplifier in these animals is strongly compromised, reducing their hearing sensitivity. This loss of function is hypothesized to derive from an abnormal structuring of the hair bundle stereocilia of the outer hair cells in bathyergids. The study demonstrated that hair bundle organization in these animals is remarkably distorted, whereas prestin-mediated hair cell motility is not confined (Pyott et al., 2020). Substitutions in genes that determine the structural integrity of hair bundles, and that are associated with hearing loss in humans, were indeed found to be accumulated in African mole-rats. Still, these substitutions show strong signatures of positive selection when compared with mice, guinea pigs and humans. Therefore, Pyott et al. (2020) interpret hearing alteration in bathyergids as adaptive, although the physiological effects of these mutations evoke the impression of degeneration.

For both bathyergid genera, Pyott et al. (2020) determined hearing thresholds that fluctuated around 60 dB SPL via the auditory brainstem response (ABR) method. Distortion product otoacoustic emissions (DPOAE), which depend on the motility of the outer hair cells and thus the functionality of the cochlear amplifier, were found to be absent in both species. Though largely consistent through the various methods applied in the study, the findings of Pyott et al. (2020) appear to be at odds with the elaborate vocal behavior of both naked and common mole-rats and with anecdotal observations in zoos and laboratories, which suggest more acute hearing (Hill et al., 1957; Ludwig and Collmar, 2009; Smith and Buffenstein, 2021; K.R.C. and S.B., personal observation). For the genus *Fukomys* in particular, the findings conflict with a significant body of work published over the last few decades (Kössl et al., 1996; Gerhardt et al., 2017; see Discussion).

In light of these discrepancies, we further investigated hearing in bathyergid mole-rats with an ABR approach, attempting to reproduce the results of Pyott et al. (2020) with naked mole-rats and *Fukomys* mole-rats. To further assess tempo and mode of the evolution of underground hearing, we also included the Chilean coruro (*Spalacopus cyanus*) in our study, which is the only fully subterranean octodontid rodent. Different from bathyergids, which might have invaded the subterranean realm in the Late Oligocene already (ca. 25 Mya; Bryja et al., 2018), coruros adopted their subterranean lifestyle far more recently in the Pliocene (ca. 3.5 Mya; Upham and Patterson, 2012). Behavioral audiograms and morphological observations on this species indicate well-developed hearing, similar in frequency range to that of diverse epigeic small mammals (Begall et al., 2004; Begall and Burda, 2006). In contrast, Pyott et al. (2020) presented evidence for a moderate accumulation of deleterious mutations in the octodontid stem lineage (however, no coruro sequence data were analyzed). This finding, together with comparative molecular data on other subterranean mammal groups (Davies et al., 2018; Pyott et al., 2020), argues for widespread hearing deficiencies in burrowers and would suggest more restricted auditory capabilities in coruros.

When extraordinarily high hearing thresholds are assumed for subterranean rodents, one would also expect that the animals vocalize using high volume (Okanoya et al., 2018). We therefore complemented our ABR recordings with measurements of the sound pressure levels of intraspecific contact calls in all three species under study.

MATERIALS AND METHODS

Subjects

We recorded ABRs from three species of social subterranean rodents, Mashona mole-rats [*Fukomys darlingi* (Thomas 1895), Nsanje population; *n*=9], naked mole-rats (*Heterocephalus glaber* Rüppell 1842; *n*=12) and coruros [*Spalacopus cyanus* (Molina 1782); *n*=12]. Individual subject data are summarized in Table 1. We classified individuals into three age groups based on established data on life history: juvenile [0–6 months (coruro)/0–12 months (Mashona mole-rat)], adult [6–48 months (coruro)/12–74 months (Mashona mole-rat)] and aged (older than adult range). All naked mole-rats were fully adult animals but of unknown exact age. None of the subjects showed apparent signs of hearing loss or behavioral disorders.

Mashona mole-rats were selected as substitutes to the Damaraland mole-rats (*Fukomys damarensis*, but see below) studied by Pyott et al. (2020), because the latter species is not available for laboratory studies in Europe. Our Mashona mole-rat laboratory strain derives from Nsanje, Southern Malawi. The animals are of comparable body size (130–200 g) to *F. damarensis*. Unpublished molecular data on this population support these animals as representatives of the species *F. darlingi* (although better known populations from Zimbabwe are dramatically smaller in body size; Bennett et al., 1994) and suggest that it forms the sister lineage to a taxon composed of *F. damarensis* and the Zambian *F. micklemi* clade (O. Mikula, personal communication), for which detailed information on hearing is already available (Gerhardt et al., 2017). We want to emphasize here that the animals used in the study by Pyott et al. (2020) derive from different captive lineages for which taxonomic identity has never been determined genetically or by aid of karyotypic methods (T. Park and R. Buffenstein, personal communication), the only ways to reliably identify *Fukomys* species in the absence of exact data on their geographic provenance (Van Daele et al., 2007). The classification of these mole-rats as *F. damarensis* is therefore questionable and needs to be verified.

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Table 1. Information on subjects participating in the study

Species	ID	Sex	Age group	No. of ABR sessions	Mass (g)
Fukomys darlingi	FD 0815	F	Aged	3	130
	FD 2229	M	Aged	3	158
	FD 3000	F	Aged	2	132
	FD 4105	F	Aged	2	130
	FD 4686	F	Aged	3	127
	FD 5361	M	Juvenile	3	59
	FD 5441	M	Juvenile	2	63
	FD 5450	F	Juvenile	1	42
	FD 9399	M	Aged	3	180
Heterocephalus glaber	HG 3105	F	Adult	1	40
	HG 5351	F	Adult	3	27
	HG 5400	M	Adult	1	49
	HG 5401*	M	Adult	2	53
	HG 5402	F	Adult	1	54
	HG 5403	F	Adult	1	43
	HG 5408*	F	Adult	2	42
	HG 5422*	M (?)	Adult	2	46
	HG 5423*	W (?)	Adult	1	27
	HG 5424*	M	Adult	1	56
	HG 67311*	M	Adult	1	32
	HG 7311*	M	Adult	1	37
Spalacopus cyanus	SC 0820**	F	Aged	2	105
	SC 2732	M	Aged	3	134
	SC 2760	M	Aged	3	126
	SC 2780	M	Aged	3	134
	SC 2797**	F	Adult	2	99
	SC 5343	M	Adult	3	127
	SC 5345	M	Adult	2	144
	SC 5346	F	Adult	3	106
	SC 5377**	M	Juvenile	3	69
	SC 7664	M	Aged	2	143
	SC 8732	F	Aged	3	96
	SC 9892	F	Adult	2	101

*Animals were tested with an additional 16 kHz step.
**Subjects were tested with an additional 36 kHz frequency step.

Subjects were housed at the University of Duisburg-Essen and were kept in a constantly heated room with a 12 h:12 h light:dark cycle, at 26±1°C constant temperature and 40–55% air humidity. All animals were socially housed and immediately returned to their home terraria after recovery from anesthesia. Enclosures were lined with wood shavings and enriched with clay pots, wooden and/or plastic tunnels, and animals were regularly offered nesting materials. Animals were kept on a staple diet of carrots and potatoes, supplemented with diverse vegetables and fruits, hay and seeds. Food was provided *ad libitum*; all studied species extract water from solids and do not drink free water.

Recordings of evoked auditory potentials

Subject preparation and monitoring

Experimental procedures were largely adopted from Gerhardt et al. (2017). ABR recordings were made between August 2020 and March 2021. Narcosis was achieved by intramuscular injection of ketamine and xylazine (mass-dependent dosage for *Fukomys* followed Garcia Montero et al. 2015, and was twice as high for *Spalacopus* and 50% higher for *Heterocephalus*), which are preferred anesthetics for ABR in small mammals (Smith and Mills, 1989; Ruebhausen et al., 2012). Whereas bathyergids close their eyes when anesthetized, coruros do not. Accordingly, their eyes were protected from desiccation by applying Vidisic® eye gel (Bausch & Lomb, Berlin, Germany). Over the time of the procedures, the subject's body temperature was maintained by a non-electric deltaphase isothermal heating pad (Braintree Scientific, Braintree, MA, USA) and repeatedly checked with a rectal electrode.

Auditory brainstem response

During testing, animals were staged in an aluminum cage (23.5×23.5×20 cm) placed within a custom-made anechoic chamber lined with foam (see Malkemper et al., 2015). All measurements as well as calibrations were performed within this chamber. A video camera installed into the chamber allowed us to monitor the animals during the tests. Brainstem potentials were recorded via subdermal electrodes (27 gauge, 13 mm, Rochester Electro-Medical, Lutz, FL, USA). The active electrode was positioned medially at the vertex of the animal, whereas the reference electrode was placed in a transverse orientation over the occipital region of the skull in close proximity to the brainstem (as in Gerhardt et al., 2017). The ground electrode was put to the subject's right thigh. Electrodes fed into a RA4LI low impedance headstage [Tucker Davis Technologies (TDT), Alachua, FL, USA] that was coupled with a Medusa RA4PA (TDT) preamplifier, both of which were positioned within the testing cage. The latter was connected to a TDT System 3 RZ6, which further amplified and digitalized recorded brainstem potentials and also generated the acoustic stimuli.

Stimulus presentation was achieved via an Arena Satellite speaker (frequency response 80 Hz to 54 kHz, used for stimuli between 200 Hz and 36 kHz; Tannoy, Coatbridge, UK) positioned approximately 20 cm from the left ear of the subject at an angle of 90 deg (the angle of sound incidence was 0 deg). Frequencies <200 Hz were emitted by a subwoofer (Punch HE Rockford Fosgate, Tempe, AZ, USA) that was positioned below the headstage level of the subject at the bottom of the anechoic chamber. Both speaker and subwoofer were operated via the RZ6. For calibration of speaker and subwoofer, a free-field microphone was employed (type 4939-C-002 with preamplifier 2669 C and conditioning amplifier Nexus 2692-A, Brüel & Kjær, Nærum, Denmark; frequency response 4 Hz to 100 kHz).

During calibration, the microphone was placed within the chamber. A dummy mimicking the volume of the respective study species was used to recreate the acoustic environment of the test situation. The microphone sensor was aligned to the position of a subject's left ear. The acoustic structure of the stimuli could be checked using a digital oscilloscope (Picoscope 4224, Pico Technology, St Neots, UK) that was jointed to the conditioning amplifier's output. Stimulus sound pressure level (SPL; reference: 20 µPa) was surveyed using the BioSig RZ software (v5.7.0, TDT), which was calibrated beforehand utilizing a Brüel & Kjær 4230 sound level calibrator with a ¼ inch microphone adaptor (B&K DB 0310). Deviations of up to 5 dB from the target sound pressure level were tolerated.

For each study species, we tested 15 different frequencies, which were preselected based on the hearing range determined by available studies on the respective species or congeneric relatives [naked mole rats: 0.03–12 kHz (16 kHz) (Heffner and Heffner, 1993; Okanoya et al., 2018), Mashona mole-rats: 0.03–16 kHz (Gerhardt et al., 2017), coruros: 0.03–32 kHz (36 kHz) (Begall et al., 2004); Table 2]. It became clear during the experiments that coruros exhibit good hearing at 32 kHz, so for three animals an additional 36 kHz step was included (noted in Table 1). Similarly, we decided to present a 16 kHz frequency step to seven naked

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Table 2. Species-specific frequencies (kHz) measured in the auditory brainstem response (ABR) set-up

Device	*Fukomys darlingi*	*Heterocephalus glaber*	*Spalacopus cyanus*
Subwoofer	0.03	0.03	0.03
	0.05	0.05	0.05
	0.1	0.1	0.1
Speaker	0.2	0.2	0.2
	0.4	0.5	0.5
	0.7	1	1
	1	2	1.3
	1.3	3	1.7
	1.7	3.5	2
	2	4	3
	4	4.5	6
	6	5	12
	8	6	16
	12	8	24
	16	12	32
		16*	36**

The device that generated the respective frequencies is listed.
*This condition was realized for seven subjects (see Table 1).
**This condition was realized for three subjects (see Table 1).

mole-rats because the duration of the anesthesia allowed us to do so without having to sedate them again. Nine frequency steps were tested in all species to allow for statistical comparisons (Table 2). Auditory stimuli were 5 ms long (1 ms rise/fall times, alternating starting phases) pure tones that were presented 12 times per second. Each frequency step comprised stimuli at nine different SPL levels that were presented with increasing intensity (0 to 80 dB, 10 dB steps). Tones were played 768 times at each SPL and the resulting recordings were averaged using the BioSig software.

All procedures were approved by the North Rhine-Westphalia State Environment Agency (permit number: 81-02.04.2019-A354).

Measurement of call amplitudes

We measured amplitudes of frequently occurring contact/greeting vocalizations, which aid in conspecific communication as general proxies for call loudness in the respective species: the naked mole-rat ‘soft chirp’, which is also known as the ‘signature call’ (n=22 from 3 individuals, mean peak frequency: ca. 3.5 kHz, cf. Okanoya et al., 2018; Barker et al., 2021), the Mashona mole-rat ‘cheep’ and ‘cluck’ vocalizations (n=20, from 2 individuals, mean peak frequencies: ca. 1.5–6.4 kHz, cf. Dvořáková et al., 2016) and the coruro ‘cooing’ vocalization (n=20, from 2 individuals, mean peak frequency: ca. 0.7 kHz, see Veitl et al., 2000).

Subjects were placed in pairs, or in the case of the naked mole-rat in groups of three individuals, in a separate glass terrarium. Call amplitudes (dB SPL) were measured with a PeakTeach® 5055 Sound Level Meter [mode: A (LO), fast adapting] that had been calibrated with a Type 4230 sound calibrator (94 dB, 1 kHZ, Brüel & Kjær). The sound level meter was moved freely by hand to maintain a close distance to the vocalizing animal. The sensor was on average positioned in a 90 deg angle at a distance of ca. 5–10 cm from the respective subject.

Threshold determination and statistics

Threshold estimation was performed by visual detection as is standard in the field (Gerhardt et al., 2017; Okanoya et al., 2018). Printouts of averaged ABR waveforms for a given frequency were assessed by three observers blind to the frequency condition. The mean estimate of the three observers was calculated and noted. Estimates were only scored when the difference between the assessed values was less than 15 dB.

All statistics were performed in RStudio (https://www.rstudio.com/). Data were checked for normal distribution employing the Shapiro–Wilk test and for homoscedasticity using the Levene test. Hearing thresholds were compared interspecifically for the nine frequencies on which all three species were tested (30 and 50 Hz, and 0.1, 0.2, 1, 2, 6, 12 and 16 kHz). Thresholds for naked mole-rats

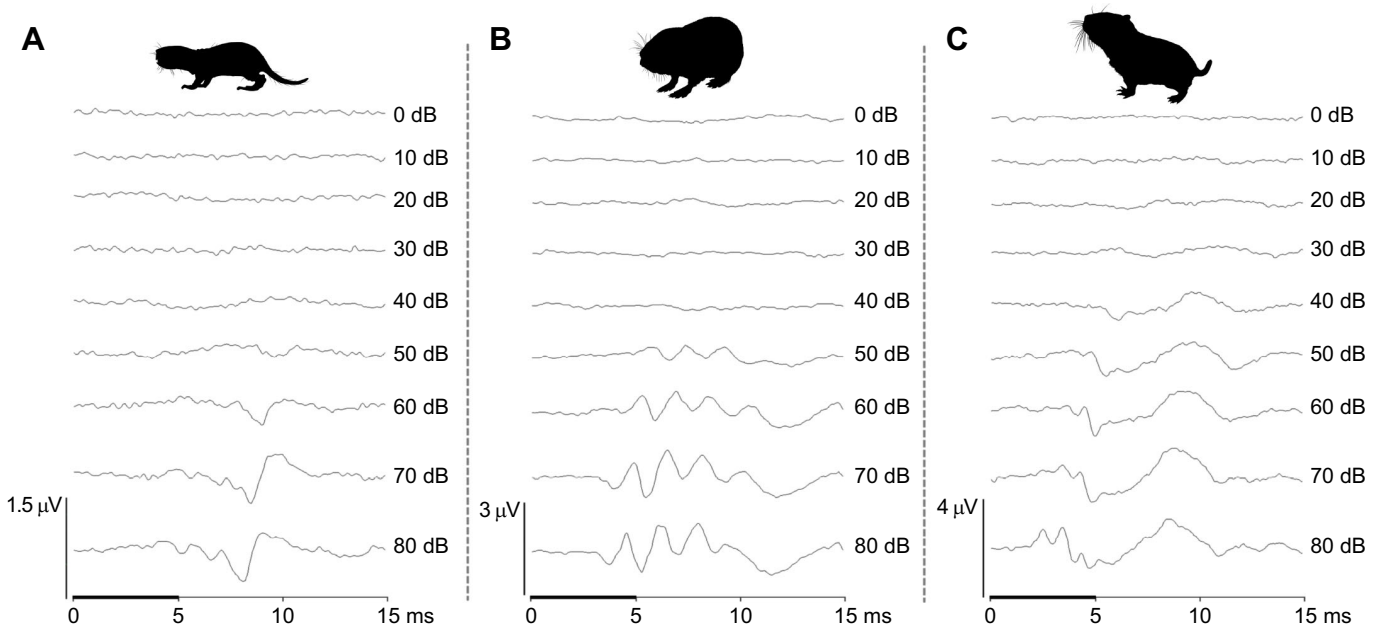

Fig. 1. Representative averaged (768×) auditory brainstem response (ABR) waveforms in the three tested subterranean rodent species. Auditory stimuli (pure tones) lasted 5 ms and are indicated in bold on the *x*-axes. (A) Naked mole-rat (*Heterocephalus glaber*, frequency shown=1 kHz); note the shallow waveform amplitude that is characteristic of this species. (B) Mashona mole-rat (*Fukomys darlingi*, frequency shown=1 kHz). (C) Coruro (*Spalacopus cyanus*, frequency shown=1.7 kHz). Silhouettes by Kai R. Caspar.

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and Mashona mole-rats were also compared at 4 kHz, a frequency at which we did not test coruros. Species-level comparisons of non-parametric data were calculated with the Kruskal–Wallis test followed by a pairwise Wilcoxon rank-sum test that employed Bonferroni correction to address for multiple comparisons. For parametric data, one-way ANOVA was used in combination with Tukey's HSD as a *post hoc* test.

To compare hearing sensitivity between age classes in coruros and Mashona mole-rats, we averaged threshold data for aged animals (n_{Coruro}=6, n_{MMR}=6), and pooled juvenile and young adult animals (n_{Coruro}=6, n_{MMR}=3). Subsequently, a Wilcoxon rank-sum test was run to compare the two groups.

RESULTS

Hearing sensitivity

Species-level ABR results are summarized in Table 3 and visualized in Fig. 2. Auditory thresholds of individual animals are listed in Table S1. The hearing range of the three studied species varied considerably at a sound intensity of 60 dB SPL, which is conventionally used as an intensity marker to denote the high- and low-frequency limits of hearing sensitivity in auditory studies (Heffner and Masterton, 1980). All species displayed a single more or less well-demarcated region of best hearing, where auditory thresholds were lowest.

The Mashona mole-rat had the most restricted hearing range, with a mean extent of 0.2–4 kHz. However, individual variation was considerable and related to age (see below). For frequencies where age-group specific average thresholds were located below 60 dB SPL, the mean (±s.d.) difference in sensitivity between aged and juvenile animals was 23.1±5.1 dB. In one aged individual, hearing thresholds were consistently located above 60 dB SPL, while one juvenile animal was still sensitive to frequencies of 6 kHz. On average, this species hears most acutely at 1 kHz, where mean hearing thresholds were found at 42.2±13.8 dB SPL. The lowest individual threshold in the sample was recorded at 1.3 kHz at 8.3 dB SPL in a juvenile animal.

In naked mole-rats, the mean hearing range extended from 0.2 to 6 kHz. The best hearing was found for frequencies between 1 and 3.5 kHz. In this range, thresholds were located at 39.6 and 43.1 dB SPL, respectively and therefore comparable to the ones of the Mashona mole-rat at a frequency of 1 kHz. The lowest recovered individual threshold was found for 3 kHz at 12 dB SPL.

The coruro had both the most acute hearing among the species in the sample and the greatest hearing range, which extended from 0.2 to 32 kHz. Sensitivity was greatest at frequencies between 1.3 and 2 kHz, where mean thresholds were recovered between 16.8 and 18.1 dB SPL. The lowest recorded threshold was 1.7 dB SPL and was found at a frequency of 1.3 kHz. Three coruros were tested on a 36 kHz step to better determine the high-frequency cut-off in this species. The mean sensitivity of these animals was 65±17.3 dB, with one juvenile animal responding at 45 dB SPL. However, mean thresholds did not differ between juvenile and adult coruros (see below).

Results from the statistical comparison of thresholds are summarized in Table S2. There were no significant differences in the hearing thresholds of the three species at frequencies of 30, 50 and 100 Hz (P>0.1). At all other tested frequencies, coruros differed significantly from the bathyergid species (P<0.05), exhibiting greater sensitivity. Hearing thresholds of naked mole-rats were consistently lower than those of Mashona mole-rats, but differences between the two species were only significant at 2 kHz (Tukey's HSD: P=0.017) and 4 kHz (Wilcoxon test: W=24.5, P=0.039).

The variation in hearing thresholds between age groups also differed between species. While coruro age classes did not differ in their hearing sensitivity (Wilcoxon test: W=116, P=0.885), younger Mashona mole-rats displayed significantly lower hearing thresholds than aged animals (W=167.5, P=0.023).

Table 3. Overview of recovered hearing thresholds of Mashona mole-rats (*Fukomys darlingi*), naked mole-rats (*Heterocephalus glaber*) and coruros (*Spalacopus cyanus*)

	Spalacopus cyanus (*n*=12)		*Fukomys darlingi* (*n*=9)		*Heterocephalus glaber* (*n*=12)	
Frequency (kHz)	Threshold (dB SPL)	s.d.	Threshold (dB SPL)	s.d.	Threshold (dB SPL)	s.d.
0.03	76.53	4.68	74.11	7.78	71.75	9.09
0.05	68.47	13.06	76.59	4.87	69.08	7.23
0.1	65.83	13.38	73.11	7.30	62.17	18.83
0.2	47.50	6.17	57.74	11.73	57.03	8.73
0.4			57.33	14.58		
0.5	35.83	8.83			49.56	13.74
0.7			49.78	13.60		
1	23.89	8.18	42.19	13.77	39.56	8.87
1.3	16.81	9.60	49.04	14.58		
1.7	18.06	7.65	54.44	15.37		
2	18.06	8.37	53.37	14.10	39.17	8.61
3	20.83	8.36			38.81	14.36
3.5					43.06	10.25
4			65.78	13.27	48.97	14.89
4.5					47.72	18.79
5					48.58	18.26
6	27.64	11.18	70.11	11.89	57.72	14.04
8			75.33	6.39	57.50	19.79
12	27.64	11.36	73.33	4.84	69.33	11.02
16	33.61	12.43	72.44	3.30	68.71	8.56
24	39.72	22.83				
32	43.19	18.26				
36	65.00	17.32				

Threshold values correspond to species means.

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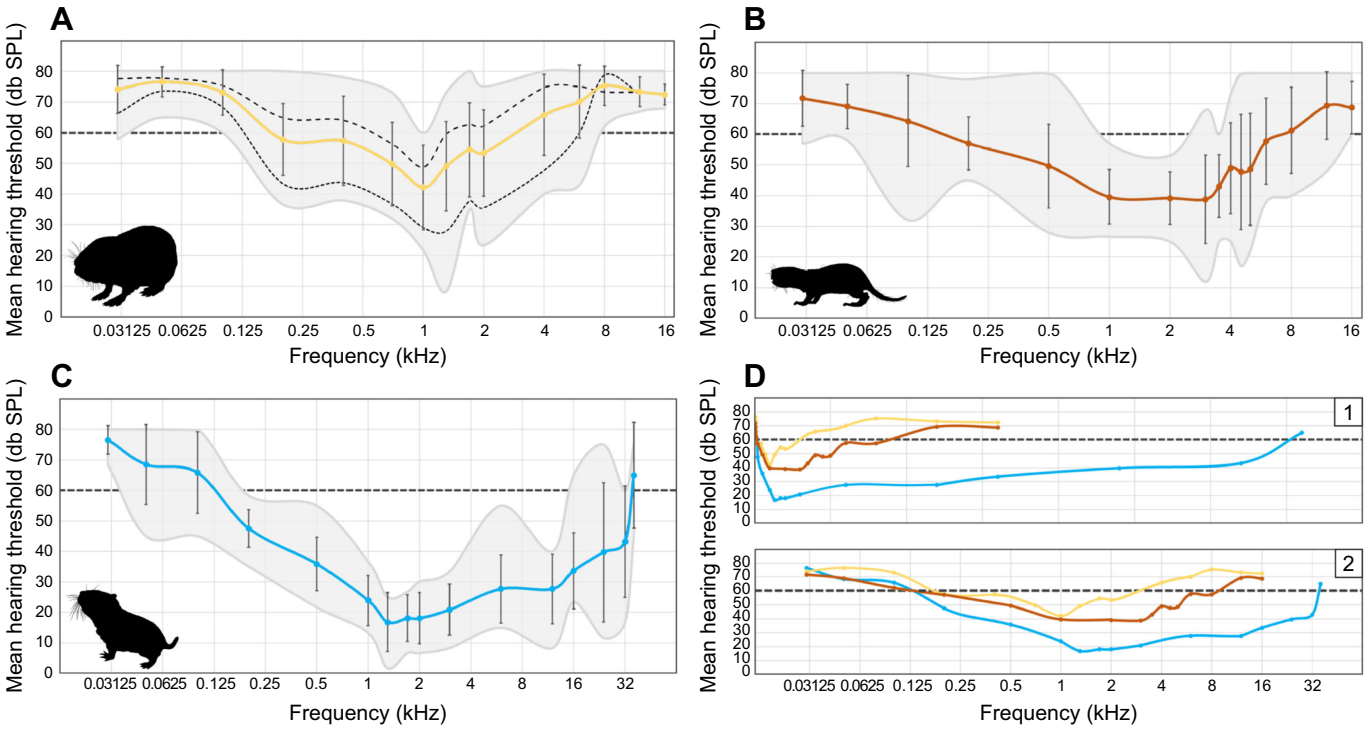

Fig. 2. Audiograms of subterranean rodents. Colored lines show mean hearing thresholds at the respective frequencies, error bars indicate standard deviations. The range of obtained threshold values is visualized by the grey overlay embedding the curves. Frequencies are plotted on $\log_2$ logarithmic scales if not indicated otherwise. (A) Mashona mole-rat (*Fukomys darlingi*). Mean hearing thresholds of aged (widely spaced dashed lines; *n*=6) and juvenile subjects (narrowly spaced dashed lines; *n*=3) are superimposed on the plot. (B) Naked-mole-rat (*Heterocephalus glaber*), *n*=12. (C) Coruro (*Spalacopus cyanus*), *n*=12. (D) Comparison of audiograms from the three species in a linear (1) and logarithmic plot (2).

Call amplitudes

Amplitudes of social vocalizations were similar overall between the three tested species (Fig. 3), despite the differences in body size and taxonomic affiliation. However, significant differences in call amplitudes still emerged (Kruskal–Wallis test: P=0.006, F=0.399). Median call amplitudes (±s.d.) were 52.6±3.3, 56.45±5.6 and 58.3 ±6.3 dB SPL for coruros, naked mole-rats and Mashona mole-rats, respectively. Pairwise comparisons showed that only coruros and naked mole-rats differed significantly in their call amplitudes (pairwise Wilcoxon test: P=0.0024; P>0.1 for other comparisons).

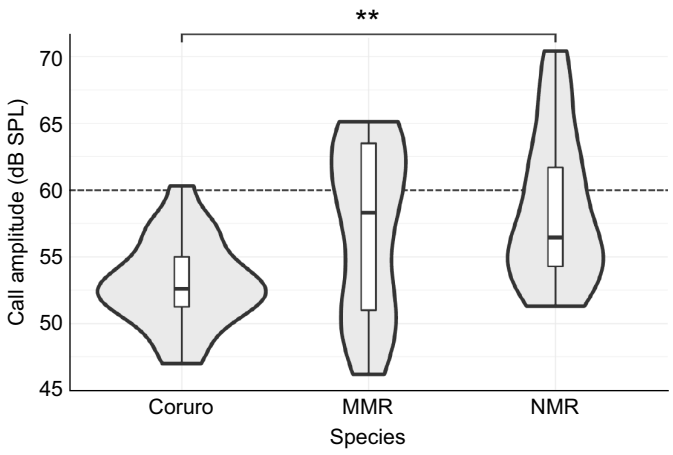

Fig. 3. Call amplitudes of subterranean rodents. MMR, Mashona mole-rat. NMR, naked mole-rat.

DISCUSSION

General discussion of results

ABRs showed marked differences in the hearing sensitivity of the three subterranean rodent species studied. The coruro differed from the two bathyergid species in displaying both a higher sensitivity, with mean thresholds below 20 dB SPL in the region of best hearing, and a far wider auditory range that reaches well into the ultrasonic domain. The ABR results for coruros are in good agreement with previously published behavioral audiograms (Begall et al., 2004). However, responses to frequencies above 20 kHz had not been tested in this species so far. Our results are the first to unambiguously demonstrate notable sensitivity to ultrasound in a hystricomorph subterranean rodent. Even at 36 kHz, one juvenile individual displayed a markedly low hearing threshold at 45 dB SPL, demonstrating that at least young coruros might have a hearing range that extends significantly further still. However, pronounced ultrasound sensitivity in coruros has already been suggested by earlier studies, for instance by cochlear frequency mapping (Begall and Burda, 2006). Nevertheless, at least for adults, the high-frequency cut-off at 44 kHz estimated by aid of this technique might need to be corrected to below 40 kHz. Besides that, it has been known that some coruro vocalizations include ultrasonic frequencies of pronounced intensity. In particular, juvenile coruros emit chirp calls that exhibit energy peaks within a frequency range of 17 to 31 kHz (Veitl et al., 2000). Although no other hystricomorph subterranean rodent is known to communicate in the ultrasonic range, several epigeic relatives of the coruro in the octodontid family are known to do so as well (*Octodon degus*: Long, 2009; *Octodontomys gliroides*: Pérez and Díaz, 2018). Sensitivity to and production of ultrasounds therefore likely

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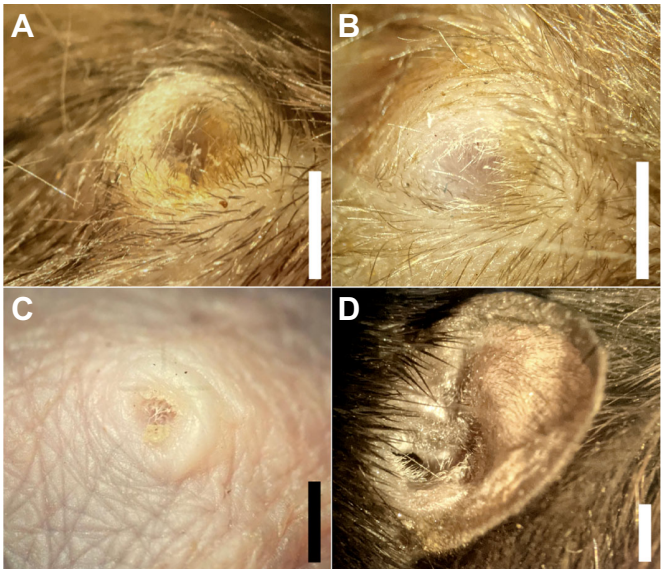

Fig. 4. The external ear in three genera of subterranean rodents. (A) *Fukomys* (adult, 4 years): the auditory meatus is narrow and lined by hair and accumulated cerumen. (B) *Fukomys* (immature, 5 months): note that cerumen is not yet obstructing the auditory meatus in the juvenile. (C) *Heterocephalus*: as in *Fukomys*, excess cerumen is well visible in the auditory meatus, which is again densely haired despite this species lacking body fur. (D) *Spalacopus*: a pinna is developed, and the auditory meatus is wide with only its entrance fringed by hair. Photographs were taken from cryopreserved specimens. Scale bars: 2 mm.

represents an ancestral trait that is still present in coruros despite their underground-dwelling habits. Accordingly, the range and sensitivity of hearing in coruros is not only greater than in other subterranean rodents (Heffner et al., 1994), but also approaches that of some fossorial and epigeic species with good low-frequency hearing such as the closely related degu (*Octodon degus*: Thomas and Tillein, 1997), the chinchilla (*Chinchilla lanigera*: Heffner and Heffner, 1991), Merriam's kangaroo rat (*Dipodomys merriami*: Heffner and Masterton, 1980), prairie dogs (*Cynomys* spp.: Heffner et al., 1994) and groundhogs (*Marmota monax*: Heffner et al., 2001). In line with this, the morphology of the coruro's middle ear exhibits only minor differences compared with epigeic caviomorph rodents, particularly the degu (Begall and Burda, 2006; Argyle and Mason, 2008). Gross morphological examination of coruros in our care also showed that these animals do not exhibit the narrow, cerumen-filled ear canals found in, for instance, bathyergids and spalacids (Fig. 4). Our results therefore corroborate the view that hearing in coruros has not undergone substantial changes in response to the invasion of the subterranean environment. Therefore, the few but presumably deleterious mutations in alleles relevant to audition that Pyott et al. (2020) described for the octodontoid lineage do not result in notable hearing impairment. Interestingly, the retainment of ultrasonic hearing sensitivity has recently been demonstrated for another geologically young subterranean rodent taxon, the Eurasian mole voles of the genus *Ellobius* (Buzan et al., 2008; Volodin et al., 2021).

Audiograms of naked mole-rats and Mashona mole-rats fit the established bathyergid pattern (Heffner and Heffner, 1993; Burda, 2006; Gerhardt et al., 2017) in displaying a pronounced restriction in audible frequencies and overall low sensitivity that did not fall below approximately 40 dB SPL, even in the regions of best hearing. The hearing curves of the two studied bathyergid species resembled each other in many respects and only diverged significantly in the 2 to 4 kHz region, where naked mole-rats exhibited more sensitive hearing. Just as in other *Fukomys* species (Müller and Burda, 1989; Gerhardt et al., 2017), the Mashona mole-rat's hearing is most responsive in a narrow frequency window at approximately 1 kHz and 40 dB SPL and its thresholds rise sharply at higher frequencies to sound pressure levels of above 60 dB at 4 kHz. Our results support the assumption that hearing sensitivity in the *Fukomys* genus is uniform despite pronounced differences in body mass between species (Gerhardt et al., 2017). In the naked mole-rat, lowest mean hearing thresholds are also located at approximately 40 dB SPL, but the region of best hearing extends from 1 to 3.5 kHz (see Okanoya et al., 2018 for similar findings) and the thresholds only approach 60 dB SPL at 6 kHz. Indeed, most calls of the remarkably vocal naked mole-rats show energy peaks in the frequency range of 2 to 4 kHz (Pepper et al., 1991; Okanoya et al., 2018). Surprisingly, both the peak and fundamental frequencies of most Mashona mole-rat calls (excluding mating calls) are centered at 2–5 kHz (Dvořáková et al., 2016) and therefore exceed the frequencies of best hearing in this species. However, the same is true for many vocalizations in congeneric species such as Ansell's mole-rat (*F. anselli*: Credner et al., 1997) and, to a lesser degree, the giant mole-rat (*F. mechowii*: Bednářová et al., 2013; cf. Gerhardt et al., 2017). Larynx size in these comparatively small-bodied mammals might constrain the production of loud low-frequency calls and could explain this discrepancy (Credner et al., 1997). Surprisingly, blind mole-rats of the genus *Nannospalax* are similar in body mass to some small-bodied *Fukomys* species but can produce lower-pitched vocalizations with peak frequencies around 0.5 kHz (Heth et al., 1986). However, blind mole-rats exhibit a Bulla thyreoidea that is not found in bathyergids, and which might act as a resonator (Credner, 1996). It remains unclear why the range of best hearing in the naked mole-rat is broader and includes higher frequencies than that in *Fukomys* (Fig. 2D). The extended total hearing range in naked mole-rats compared with *Fukomys* cannot be deduced from the morphology of the middle ear ossicles and the bony labyrinth. The structure of the incudo–mallear complex as well as the less developed cochlear coiling in the naked mole-rat have been proposed previously to indicate worse audition in this species than is found in other bathyergids (Mason et al., 2016).

Despite stark differences, there are also important similarities between all three studied taxa. Bathyergids and coruros converge in that the region of best hearing is located between or at least includes the frequency range 1 and 2 kHz. In that regard, the data are in agreement with previous audiograms of subterranean rodents (Heffner and Heffner, 1993; Begall et al., 2004; Burda, 2006), which all showed highest sensitivities in that unusually low frequency range and a more restricted range of best hearing than many other small mammals (Heffner and Masterton, 1980; Heffner et al., 1994). These peculiar peak sensitivities correspond well with the tunnel acoustics of the subterranean environment (Lange et al., 2007; Okanoya et al., 2018).

We recovered significant differences in hearing thresholds between juvenile and aged animals in the Mashona mole-rat, but not between coruro age groups. On the one hand, this discrepancy could relate to the fact that age differences in the Mashona mole-rats were far more pronounced than in the coruros and therefore do not necessarily point to varying influences of age on hearing sensitivity in the two groups. On the other hand, different from coruros, African mole-rats accumulate cerumen in their ear canals, which is expected to gradually worsen auditory performance in older individuals (Fig. 4; compare Kössl et al., 1996). We suggest that such a cerumen plug contributes importantly to the observed

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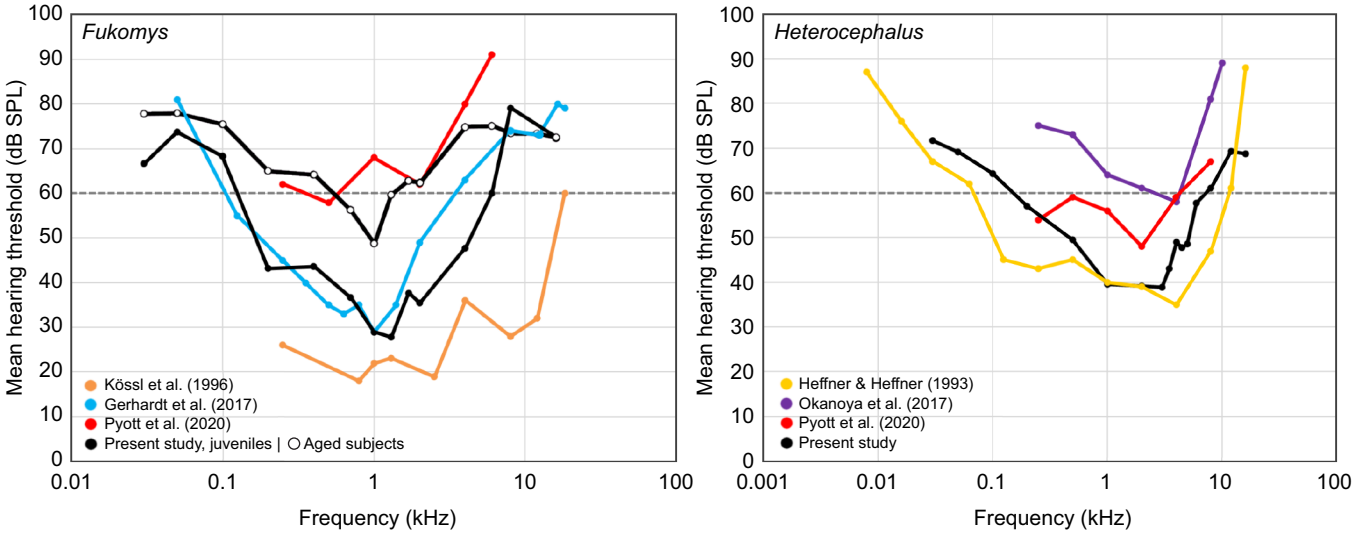

Fig. 5. Hearing curves for northern common mole-rats (*Fukomys*) and naked mole-rats (*Heterocephalus*) from various studies and obtained with different methodologies. Names in brackets refer to the respective species of *Fukomys* tested. Pyott et al. (2020) – ABR [*F. damarensis* (?)]. Gerhardt et al. (2017) – ABR (*F. anselli*). Kössl et al. (1996) – distortion product otoacoustic emissions (DPOAE) (*F. anselli*). Okanoya et al. (2018) – ABR. Heffner and Heffner (1993) – behavioral audiogram. Present study – ABR (*F. darlingi*), differentiated into aged and juvenile age groups. Dotted lines indicate 60 dB SPL.

differences between Mashona mole-rat age groups. Different from adults, we observed no cerumen at the opening of the auditory meatus in juvenile *Fukomys* (Fig. 4). However, we cannot infer to what extent this difference among age classes is connected to cerumen accumulation instead of to impairments of the organ of Corti that progress as senescence advances (Yamasoba et al., 2013). The hearing curve that we recovered for juvenile *Fukomys* is very similar to the ones described by Gerhardt et al. (2017), who tested mole-rats that were up to 175 weeks (3.35 years) old (Fig. 5). Hence, we expect that in animals up to this age, cerumen plugs do not impair hearing. Although demographic data on wild *Fukomys* are sparse, there is preliminary evidence that few free-ranging individuals actually reach such an age (Schmidt et al., 2013). Hence, we tentatively suggest that the thresholds recovered for juveniles are more representative for the majority of animals in the wild than the ones we describe for aged subjects.

Fitting its higher hearing sensitivity, calls in the coruro were fainter than in the bathyergids, but the loudness of measured vocalizations was still surprisingly similar in the three species, given their different taxonomic affinities and body sizes. Expectedly, call amplitudes were located well in the range of species-specific hearing that we recovered in the ABRs for the respective peak frequencies. However, the median call amplitudes of bathyergids are, if at all, barely loud enough to be audible if hearing sensitivities recovered in other studies, especially those in Pyott et al. (2020), are considered. Along with other inconsistencies across papers on hearing in bathyergids, this issue requires further discussion.

How strongly impaired is hearing in African mole-rats?

The acuity and physiology of hearing in the African mole-rats of the family Bathyergidae have been studied intensively, but with striking differences in specific outcomes. All reports agree that both hearing sensitivity and range are extremely restricted in bathyergids compared with epigeic rodents, but it is not yet clear which physiological traits cause this difference. Our results on Mashona mole-rats agree with previous electrophysiological hearing studies by Müller and Burda (1989) and Gerhardt et al. (2017) on congeneric species (Fig. 5). However, we recovered in part drastically lower sensitivities than suggested by behavioral audiograms for *Fukomys* (Brückmann and Burda, 1997).

Behavioral audiograms typically (but not always) yield thresholds approximately 5–15 dB lower than ABRs, which has been explained as a side effect of anesthesia (Smith and Mills, 1989; Ramsier and Dominy, 2010; Sisneros et al., 2016; Gerhardt et al., 2017). However, differences in outcome between the two methods are supposed to be most pronounced at low frequencies and are expected to diminish or even revert with increasing frequency (Ramsier and Dominy, 2010; Sisneros et al., 2016). This is not a consistent pattern in bathyergids (Gerhardt et al., 2017). The only available behavioral audiogram for *Fukomys* by Brückmann and Burda (1997) reports good hearing at high frequencies beyond 10 kHz with thresholds located 30 dB to more than 40 dB lower than those recovered in electrophysiological studies, including this one, in that tonal range. Gerhardt et al. (2017) already pointed out critical methodological issues with this study that could explain these inconsistencies and which we do not reiterate here. Replication of these results is required to eventually establish a reliable behavioral audiogram for *Fukomys*. Instead, our ABR results for naked mole-rats show good overall agreement with the established behavioral audiogram (Heffner and Heffner, 1993; Fig. 5). If we compare the alignment of the two curves with audiograms of other species obtained with these two methods, they fit well into the spectrum of agreement (Ramsier and Dominy, 2010).

On first glance, our data do also not appear to align with the results of a DPOAE study on Ansell's mole-rats (*Fukomys anselli*), which recorded responses to frequencies as high as 18 kHz and low peak sensitivities below 20 dB SPL (Kössl et al., 1996; see Fig. 5). Here, the recovered hearing sensitivity showed a similar range to the behavioral audiogram for common mole-rats, but was on average approximately 10 dB greater (Brückmann and Burda, 1997). Gerhardt et al. (2017) explained the discrepancies between the results of Kössl et al. (1996) and ABR-derived data by the fact that DPOAE measurements required the mole-rat auditory meatus to be cleaned and widened. Otherwise, the faint otoacoustic emission signals could not be picked up. With cleaning, hair and accumulated cerumen was removed, which attenuates incoming sounds and

likely acts as a low-pass filter, preventing high frequencies to penetrate deeper into the ear (Kössl et al., 1996). Similarly obstructed ear canals have been observed in spalacid blind mole-rats and, to a lesser degree, also in naked mole-rats (Burda et al., 1992; Mason et al., 2016). The DPOAE results are therefore in line with the notion that the poor hearing of common mole-rats is significantly influenced by the sealed auditory meatus and therefore do not contradict the ABR data reported by us and other previously mentioned authors.

In contrast to Kössl et al. (1996), Pyott et al. (2020) found markedly higher thresholds in ABR set-ups for naked mole-rats and *Fukomys* mole-rats than we did, and failed to obtain DPOAE signals from either species (see also Okanoya et al., 2018 for even higher ABR thresholds in *Heterocephalus*; Fig. 4). The *Fukomys* mole-rats studied by Pyott et al. (2020) displayed thresholds barely falling below 60 dB SPL. If the latter results are representative, *Fukomys* mole-rats would, even when considering the threshold elevation caused by ABR measurements, be barely able to hear many of their social vocalizations, which, as we show, are mostly fainter. In light of the results of Kössl et al. (1996), it is remarkable that Pyott et al. (2020) found no evidence for DPOAE in *Heterocephalus* or *Fukomys*. A lack of DPOAE would imply that the cochlear amplifier, which is dependent on the motility of the outer hair cells in the organ of Corti and their linkage to the tectorial membrane by stereocilia, is non-functional (Pyott et al., 2020). Although we concur with the assumption that stereocilial defects are likely involved in the poor hearing of bathyergids and perhaps also other burrowing rodents (cf. Raphael et al., 1991), we doubt that the cochlear amplifier in these animals is non-functional and that their hearing thresholds are generally as high as reported by Pyott et al. (2020).

A major issue of this hypothesis is that it cannot explain the findings of Kössl et al. (1996), who worked with Ansell's mole-rats (*Fukomys anselli*). Although Pyott et al. (2020) do not present molecular data on Ansell's mole-rats, the study shows that relevant mutations potentially affecting the cochlear amplifier are shared by all *Fukomys* species and do not vary among congeners. It is extremely unlikely that critical mutations reversed solely in the Ansell's mole-rat lineage. Particularly, because Pyott et al. (2020) report no sign of such a reversal in Micklem's mole-rat (*Fukomys micklemi*), a recently diverging sister species of *F. anselli* (Van Daele et al., 2007). Pyott et al. (2020) were aware of the study by Kössl et al. (1996) but reported no obstruction of the auditory meatus by cerumen and hairs in the two bathyergid genera studied. Accordingly, they did not clean the ear canals of their subjects. Clean ear canals in adult bathyergids would be surprising in light of both the observations by other authors (Burda, 2006; Mason et al., 2016; see Fig. 4) and the high thresholds that the same study recovered for these animals in the ABR set-up (Fig. 5). Pyott et al. (2020) studied 5-year-old mole-rats, in which some cerumen accumulation must be expected. Thus, undetected remnants of cerumen sealing the auditory meatus could potentially explain the lack of DPOAEs in the tested species. Pyott et al. (2020) propose that the differences between Ansell's mole-rat and their tested *Fukomys* species, which were classified as Damaraland mole-rats, could result from hearing specializations in the former. These would include greater hearing sensitivity in conjunction with a region of increased hair cell density and, therefore, frequency representation in the apical regions of the cochlea. However, hair cell densities follow the same pattern in the Damaraland mole-rat and are indeed uniformly expressed in *Fukomys* species as well as in the sister genus *Cryptomys* (Lange, 2006). As shown by Gerhardt et al. (2017), Ansell's mole-rats do not hear significantly better than congeneric species, which is also suggested by our results. Instead, the mole-rats tested by Pyott et al. (2020) exhibit remarkably poor hearing, which is roughly comparable to that in our aged subject group, despite them being significantly younger (5 years versus >10 years, see Fig. 5). Therefore, the respective data do not appear to be generally representative of *Fukomys*.

We want to emphasize a procedural difference between our approach and the works of Pyott et al. (2020) and Okanoya et al. (2018), which could explain the varying outcomes on hearing sensitivity in *Heterocephalus* and *Fukomys*. Both studies used dosages of anesthetics that far exceeded those we employed here: 80 mg kg^{-1} ketamine and 20 mg kg^{-1} xylazine (Pyott et al., 2020) and 35–50 mg kg^{-1} ketamine and 8 mg kg^{-1} xylazine (Okanoya et al., 2018), compared with 6 mg kg^{-1} ketamine and 2.5 mg kg^{-1} xylazine for *Fukomys* and 9 mg kg^{-1} ketamine and 3.4 mg kg^{-1} xylazine for *Heterocephalus*. The dosages used by Pyott et al. (2020) and Okanoya et al. (2018) were comparable to or even higher than those applied to murine rodents to record ABR (Cederholm et al., 2012; Ruebhausen et al., 2012), although these have an elevated metabolic rate compared with bathyergids (Šumbera, 2019). We are unaware of studies that compared the effects of varying ketamine/xylazine volumes on ABR outcomes in small mammals but believe that such extreme differences in dosage could have contributed significantly to the high hearing thresholds communicated in the aforementioned studies. Kössl et al. (1996) found that ketamine dosages above 50 mg kg^{-1} also have a diminishing effect on DPOAE in Ansell's mole-rats. However, even at significantly higher dosages (90 mg kg^{-1}) comparable to the ones applied by Pyott et al. (2020), DPOAE were still detectable, so the differences in anesthesia protocols cannot explain why the latter study found no evidence at all for DPOAE in bathyergids (Kössl et al., 1996).

It should also be noted that the morphology of the organ of Corti in animals from the *Fukomys* laboratory strain used by Pyott et al. (2020) is aberrant, as these animals exhibit supernumerary outer hair cells (see Lange, 2006 for a comparison with wild-caught *F. damarensis*) and other unusual features relating to hearing physiology (Barone et al., 2019; Pyott et al., 2020). It therefore remains unclear whether the results of Pyott et al. (2020) on *Fukomys* in both the DPOAE and ABR set-ups might have been biased by pathologies.

To conclude, although Pyott et al. (2020) advanced the field in many regards and provide convincing arguments that the insensitive hearing in bathyergids relates at least in part to hair bundle defects, methodological issues, conflicting data from other studies, and anecdotal reports from diverse settings and localities (Ludwig and Collmar, 2009; Smith and Buffenstein, 2021) suggest that their auditory performance is not as poor as reported by these authors. Whether the cochlear amplifier is indeed non-functional in bathyergids needs to be clarified by future studies and can be doubted in light of the findings by Kössl et al. (1996).

Implications for the evolution of hearing in burrowing rodents

Comparisons between coruros and more ancient burrowing groups such as African mole-rats or blind mole-rats are valuable to infer how changes in hearing physiology relate to the ecological transition to the subterranean realm. Can our results advance the debate on whether hearing evolution in subterranean rodents follows adaptive or degenerative paths?

The hearing range and sensitivity of the coruro appear to be very similar to those of epigeic caviomorph rodents, which implies that a

subterranean lifestyle per se does not produce selection pressures that induce a quick adaptation to the underground environment. Neither the low high-frequency cut-offs nor high hearing thresholds known from African mole-rats, blind mole-rats and pocket gophers (Heffner and Heffner, 1993) are found in coruros. However, compared with non-burrowing caviomorph rodents such as the chinchilla and the guinea pig (Heffner et al., 1971; Heffner and Heffner, 1991), the coruro displays a more restricted range of best hearing that is strongly shifted towards lower frequencies. This difference could represent a fast-evolving hearing adaptation of subterranean rodents as it appears restricted to and is present in all obligate underground-dwelling species studied so far (Burda et al., 1992; Heffner and Heffner, 1993). In fossorial rodents, such as ground squirrels, a similar shift and restriction of the region of best hearing is not evident (Heffner et al., 1994, 2001). However, as little is known about hearing sensitivity in epigeic octodontids, we cannot be sure how strongly the coruro really diverges from its ancestral family pattern.

Despite its subterranean and highly social lifestyle, hearing thresholds in coruros remain low. This is at odds with the hypothesis that the reduction of peak hearing sensitivity observed in most subterranean rodents is an adaptation to protect the ear from overstimulation by low-frequency vocalizations amplified in the burrow environment (Burda et al., 1992; Lange et al., 2007). There are further arguments against this notion. First, subterranean rodents communicate predominantly over short distances within their burrow systems (see Amaya et al., 2016 for an exception). The social bathyergids, for instance, almost exclusively vocalize when conspecifics are immediately close by and in tactile range, precluding sound amplification from affecting at least the main addressee of the vocal signal. Besides that, prolonged social encounters mostly occur in the nest chamber of the burrow system, which, owing to its shape and bedding, is expected to exhibit acoustic properties very different from those of tunnels. As already remarked by Mason (2013), this hypothesis also conflicts with the fact that subterranean rodents have lost, or in the case of the coruro (Begall and Burda, 2006), severely reduced, one of the two mammalian middle ear muscles, which otherwise could protect the ear from overstimulation (but see Burda et al., 1992 and Mason, 2006 for the possibility that middle ear muscles are maintained in epigeic groups to allow the ear to better adapt to high frequencies – an obsolete capacity underground). It is also difficult to argue for an adaptive value of high thresholds in the low-frequency region because the sensitivity of epigeic mammals in respective frequency ranges does often not notably differ (Heffner and Heffner, 1993) or is even higher than in subterranean groups (Heffner and Masterton, 1980). Instead, it appears that an ancestral hearing sensitivity is retained in the low-frequency range, while thresholds gradually increase towards higher frequencies, which is compliant with tunnel acoustics (Lange et al., 2007; Okanoya et al., 2018).

Yet, the coruro, mole-voles (Volodin et al., 2021) and, to a lesser extent, fossorial ground squirrels (Heffner et al., 1994; Jackson et al., 1997; Heffner et al., 2001) demonstrate that the loss of high-frequency hearing in underground environments does not evolve fast. The example of the mole-voles illustrates that even if the middle ear is optimized to process low frequencies, ultrasound vocalizations can still constitute an important aspect of intraspecific communication in subterranean rodents (Lange et al., 2004; Volodin et al., 2021). It is therefore doubtful that the extreme hearing range restriction in groups such as bathyergids and spalacids represents a trade-off to enable responsiveness to low frequencies underground. The delayed loss of high-frequency sensitivity could therefore be interpreted in favor of the degeneration model of hearing evolution in subterranean mammals.

An obstruction of the outer ear canal by hair and cerumen, as observed in diverse subterranean mammals, will notably contribute to poor hearing (Fig. 4; see previous section). However, the question of whether this trait serves an adaptive function is not resolved. Burda (2006) suggested that partially sealed auditory meatus represents an adaptation to prevent debris from entering, particularly when pinnae are absent. However, the occurrence of that character among subterranean mammals is not universal and can fluctuate even between closely related groups. For instance, the ear canals in the European mole (*Talpa europaea*) are typically unobstructed, whereas they are filled with cerumen in American mole genera (Mason, 2006). In groups sensitive to ultrasound, a sealed auditory meatus would be surprising, as it likely constitutes a substantial low-pass filter (Kössl et al., 1996). Indeed, we did not observe cerumen plugs in coruros (Fig. 4) and do not expect them to be found in the pinna-less mole-voles that communicate in the ultrasound range as well. Therefore, the sealing of the auditory meatus and its effect on hearing could represent a burrowing adaptation or reflect a neutrally selected deregulation of ear secretion in this peculiar habitat. In any case, it is difficult to argue that it evolved as an adaptive trait to facilitate hearing underground.

Besides all these factors, it is crucial to consider the genetic underpinnings of hearing in burrowing rodents. Some studies have reported positive selection for loci involved in hearing and outer hair cell hair bundle integrity in subterranean mammals (for instance ADGRV1 and USH1C; Davies et al., 2018; Pyott et al., 2020). Respective alleles have been speculated to benefit low-frequency hearing (Pyott et al., 2020). However, it remains unclear how that is realized, particularly because there is no plausible mechanism for hair bundle defects granting such an advantage. Counterintuitively, disintegration or even the absence of hair bundles is most frequent in the apical regions of the cochlea in spalacids and bathyergids, where low frequencies are processed (Raphael et al., 1991; Pyott et al., 2020).

From a proximate perspective, hair bundle defects and obstructed ear canals can explain important aspects of the poor hearing in various subterranean rodents, but why these traits arose in an evolutionary context remains elusive. Until the influence of candidate genes affecting hearing in burrowing mammals is better characterized, it will be difficult to determine whether specific derived hearing traits in these animals are due to adaptation, degeneration or perhaps even pleiotropy. Future research should consider including more epigeic species as a comparison to burrowing relatives in order to clarify the potential adaptive value of specific alleles. Interestingly, the hearing gene mutations listed by Pyott et al. (2020) are not restricted to subterranean mammals, but were also found to be drastically accumulated in African cane-rats (*Thryonomys* spp.), which are closely related to bathyergids. Different from mole-rats, these large-bodied rodents are fully epigeic and only occasionally dig shallow burrows in areas lacking the dense vegetation they prefer to hide in (Kingdon, 1974; erroneously denoted as fossorial by Pyott et al., 2020).

While awaiting further data on the interplay of genetics and hearing physiology, we suggest being open to both adaptive and degenerative interpretations of specific auditory traits in subterranean rodents. Given the evidence laid out above, we would argue that the elevated hearing thresholds and loss of high-frequency hearing found in these animals reflect a lack of selective pressures to maintain sensory characteristics that evolved in epigeic ancestors. In contrast, the consistent low-frequency shift of the area

of best hearing that is already observable in geologically young lineages such as the coruro, is likely an adaptation to the peculiar acoustics of the underground realm. Ultimately, crucial questions about the hearing of burrowing rodents remain unresolved despite ongoing research efforts. Building on recent multidisciplinary approaches (Pyott et al., 2020), these issues need to be addressed by combining behavioral, physiological and genetic data to obtain a holistic picture of how and why these animals perceive the world in the way they do.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: K.R.C., S.B.; Methodology: K.R.C., P.G., S.B.; Formal analysis: K.R.C.; Investigation: K.R.C., A.H., L.M., S.B.; Data curation: K.R.C., A.H., L.M.; Writing - original draft: K.R.C.; Writing - review & editing: K.R.C., A.H., L.M., P.G., S.B.; Visualization: K.R.C.; Supervision: S.B., P.G.

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