

## Habitat influence on the evolution of male mating vocalizations in subterranean and surface-dwelling rodents (Rodentia)

Ema HROUZKOVÁ<sup>1</sup> & Cristian Eric SCHLEICH<sup>2</sup>

<sup>1</sup> Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 1760, CZ–370 05 České Budějovice, Czech Republic

<sup>2</sup> Laboratorio Ecofisiología, Universidad Nacional de Mar del Plata, IIMyC-Conicet, Argentina

received on 10 October 2022

**Abstract.** The acoustic adaptation hypothesis (AAH) is often tested between species from open and closed habitats. However, the acoustic differences are rather small and thus the evidence is ambiguous. We tested the AAH between subterranean and surface-dwelling species living in very different acoustic environments. Lower frequencies (<1 kHz) are transmitted best in subterranean burrows and there is a high-frequency cut off around 3 kHz. The other important factor influencing the frequencies of vocal signals is body size. Acoustic allometry – a negative relationship between body size and frequency of acoustic signals – indicates that larger species tend to produce sounds of lower frequencies than smaller species, due to their larger vocal apparatus. The present study shows, that acoustic allometry applies to subterranean as well as surface-dwelling rodents and that the environment influences the main frequency of their vocalization. Besides, the subterranean species tend to have lower vocal signals than surface-dwelling species.

**Key words.** Acoustic allometry, acoustic adaptation hypothesis, subterranean rodents.

### INTRODUCTION

Acoustic communication plays a major role in many species of animals (BRADBURY & VEHCAMP 1998). The physical properties of acoustic signals, mostly frequency and duration, constitute key factors in their propagation through the environment (MORTON 1975, WILEY & RICHARDS 1982, PADGHAM 2004). Usually, long low-frequency sounds are less attenuated during transmission than those of higher frequencies (WILEY & RICHARDS 1982, PADGHAM 2004). However, the problem is far more complicated, the explanation for the physical characteristics of sounds produced by diverse species is proposed by different, and sometimes complementary, hypotheses: (1) the acoustic adaptation hypothesis, and (2) the morphological constraint hypothesis.

The acoustic adaptation hypothesis (AAH) predicts that frequencies of animal vocalization should be adapted to the acoustic environment to maximise the effectiveness of sound transmission (MORTON 1975, HANSEN 1979, RICHARDS & WILEY 1980). The sounds transmitted through the natural environment are subject to degradation, for example due to environmental absorption, reverberation and scattering. The degree of degradation depends both on the sound structure and on the acoustic characteristics of the environment (WILEY & RICHARDS 1982, BRUMM & NAGUIB 2009). Most papers dealing with AAH focus on the differences between open

doi: 10.37520/lynx.2022.012

and closed habitats, with higher frequencies being attenuated more strongly in closed habitats (MORTON 1975, MARTEN & MARLER 1977, WILEY & RICHARDS 1978). Hence, forest species should display lower frequencies vocalizations compared to species living in open habitats (MORTON 1975, EY & FISCHER 2009). However, evidence supporting this hypothesis is scarce, and it seems that the habitat-related adjustments of frequency parameters of acoustic signals of birds, anurans and mammals are not as widespread as previously thought (EY & FISHER 2009, GARCÍA-NAVAS & BLUMSTEIN 2016, HARDT & BENEDICT 2020, MIKULA et al. 2021).

The morphological constraint hypothesis basically states that acoustical signals produced by the individual are limited by its body size (RYAN & BRENOWITZ 1985, BRADBURY & VEHRINCAMP 1998, FITCH & HAUSER 2002). Acoustic allometry, the negative relationship between body size and frequency of acoustic signals, indicate that larger species tend to produce sounds of lower frequencies compared to smaller species, a general rule in animal bioacoustics that has been documented across various groups, including insects, fishes, amphibians, reptiles, birds and mammals (WALLSCHLÄGER 1980, MCCLATCHIE et al. 1996, FITCH & HAUSER 2002, GILLOOLY & OPHIR 2010, GARCÍA-NAVAS & BLUMSTEIN 2016, PEARSE et al. 2018). Particularly in mammals, this limitation in the frequency range of vocalizations may be caused directly by the morphology of the vocal apparatus (FITCH & HAUSER 1995, TAYLOR & REBY 2010). Both the frequency at which vocal folds vibrate and at which the air resonates depends on the length of the vocal tract, with longer ones producing sounds of lower frequencies (BOWLING et al. 2017). The duration of the vocalizations could be also limited by the size of the individual as well, the larger the animal is the longer the call could be due to the larger lung volume (FITCH & HAUSER 1995, EY et al. 2007). However, this theory was tested only interspecifically with mixed results (HAMMERSCHMIDT et al. 2000, EY et al. 2007).

One interesting aspect of the AAH is that it has usually been tested in little divergent acoustic habitats, commonly comparing among closed and open environments. One way to overcome this situation is by making comparisons between two very different acoustic locations. In this sense, the acoustic environment of the subterranean burrows is unique and offers an excellent opportunity to validate the AAH in contrasting habitats. In tunnels of subterranean rodents, the best propagated frequencies are around 400–800 Hz, while higher frequencies are strongly attenuated. This is very different from any type of aboveground acoustic environment (HETH et al. 1986, LANGE et al. 2007, SCHLEICH & ANTENUCCI 2009). Another peculiarity of the subterranean acoustic environment is that there is no need to localize the source of sound, since it can come only from the front (HEFFNER & HEFFNER 1993). Therefore, subterranean species should use lower frequencies than would correspond to the size of their hearing apparatus, being limited only by the size of their vocal apparatus (FITCH & HAUSER 1995, TAYLOR & REBY 2010).

Alarm calls are mainly used to test AAH (but also the morphological constrained hypothesis) as they are used for long range communication and should be adapted to the acoustic environment (GARCIA-NAVAZ & BLUMSTEIN 2016). Also, they can be easily recorded from numerous species of mammals. However, several species of subterranean rodents do not use alarm calls. On the other hand, mating or courtship calls are present in all subterranean species studied so far (PEPPER et al. 1991, CREDNER et al. 1997, KNOTKOVÁ et al. 2009, BEDNÁŘOVÁ et al. 2013, VANDEN HOLE et al. 2014, DVOŘÁKOVÁ et al. 2016, BARKER et al. 2021). Variation in mating calls can cause genetic differences and thus speciation (CAMPBELL et al. 2010, PUECHMAILLE et al. 2011, AHONEN et al. 2018), therefore it is crucial for reproductive individuals to receive and evaluate information contained in them without any distortion. As a consequence, mating calls should be tuned to the area of best hearing, which should, on the other hand, be tuned to

match the acoustic environment (CHARLTON et al. 2019). Male mating calls are also important signals of the male quality and size, and in most of the species they are honest with the exception of several cervids and primates with descended larynx (LIEBERMAN 1984, FITCH & REBY 2001).

Therefore, and in order to study the probable effects of physical and environmental constraints on the design of rodent vocalizations, we decided to explore acoustic characteristics of male mating vocalizations of various species of subterranean and surface-dwelling rodents in relation to their body size. The comparison of mating calls, that can be considered as honest signals of body size, among subterranean and aboveground rodent species will enable us to test hypotheses dealing with the main frequency and duration of the vocalizations: (a) above and subterranean species will display a negative relationship between call frequency and body mass, (b) subterranean species will display vocalizations of lower frequencies due to the specific acoustic environment in their burrows, (c) duration of calls will be longer in bigger individuals irrespective of their habitat.

## MATERIALS AND METHODS

Acoustic properties of male mating calls from 27 species of rodents were obtained directly from our own recordings or from published material in scientific journals or thesis (Table 1). In particular, we obtained information of main frequency (MF, frequency carrying maximum energy) and note duration (D) of male mating vocalizations, and mean body weight for males of each species. Body weight (BW) is considered to be a key factor in the evolution of acoustic signaling in mammals (FITCH 2000, MARTIN et al. 2016). Finally, rodent species were classified according to their lifestyle, subterranean or surface-dwelling (Table 1).

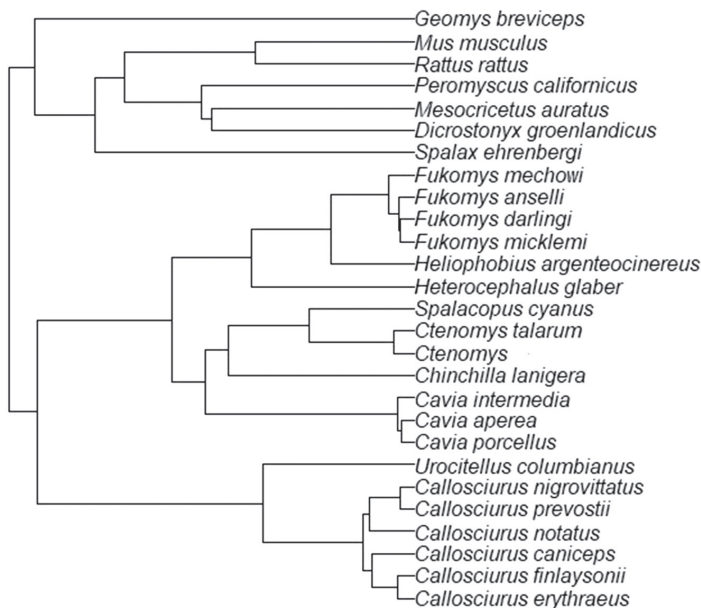


Fig. 1. Phylogenetic tree of the subterranean and surface-dwelling species used in this study.

Table 1. Body mass (g), main frequency (MF), duration (s) of male mating vocalizations for the 27 rodent species utilized in this study, including information on their lifestyle; W – body weight (g)

species	W	mf (hz)	duration (s)	lifestyle	references
<i>Mus musculus</i>	15.0	62800	0.074	surface	GOURBAL et al. (2004)
<i>Dicrostonyx groenlandicus</i>	40.0	25000	0.07	surface	BROOKS & BANKS (1973)
<i>Heterocephalus glaber</i>	40.2	4958	0.152	subterranean	BARKER et al. (2021)
<i>Peromyscus californicus</i>	41.0	40000	0.173	surface	BRIGGS & KALCOUNIS-RUEPPELL (2011)
<i>Fukomys anelli</i>	92.6	2000	ND	subterranean	CREDNER et al. (1997)
<i>Spalacopus cyanus</i>	98.0	320	0.03	subterranean	VEITL et al. (2000)
<i>Mesocricetus auratus</i>	104.0	32000	0.0095	surface	FLOODY & PFAFF (1977)
<i>Rattus rattus</i>	133.0	48900	0.003	surface	White et al. (1990)
<i>Ctenomys talarum</i>	140.0	400	0.029	subterranean	SCHLEICH & BUSCH (2002)
<i>Fukomys darlingi</i>	158.7	1500	0.03	subterranean	DVOŘÁKOVÁ et al. (2016)
<i>Spalax ehrenbergi</i>	170.0	568	0.025	subterranean	HETH et al. (1988)
<i>Geomys breviceps</i>	190.0	1828	0.275	subterranean	DEVRIES & SIKES (2008)
<i>Callosciurus notatus</i>	210.0	7043	0.19	surface	TAMURA (1993)
<i>Callosciurus nigrovittatus</i>	210.0	2896	0.18	surface	TAMURA et al. (2018)
<i>Heliophobius argenteocinereus</i>	225.5	1530	0.06	subterranean	KNOTKOVÁ et al. (2009)
<i>Ctenomys sp.</i>	241.0	300	0.048	subterranean	AMAYA (2016)
<i>Callosciurus erythraeus</i>	270.0	2341	0.24	surface	TAMURA et al. (2018)
<i>Callosciurus fynlaisonii</i>	278.0	2282	0.24	surface	TAMURA et al. (2018)
<i>Callosciurus caniceps</i>	280.0	3030	0.06	surface	TAMURA (1993)
<i>Callosciurus prevostii</i>	400.0	4176	0.09	surface	TAMURA et al. (2018)
<i>Fukomys mechowii</i>	432.8	680	0.04	subterranean	BEDNÁŘOVÁ et al. (2013)
<i>Urocitellus columbianus</i>	480.0	3000	0.65	surface	MANNO et al. (2007)
<i>Chinchilla laniger</i>	500.0	387	ND	surface	BARTL (2006)
<i>Cavia aperea</i>	550.0	135	0.034	surface	MONTICELLI (2011)
<i>Cavia intermedia</i>	618.0	399	0.025	surface	VERZOLA-OLIVIO & MONTICELLI (2017)
<i>Cavia porcellus</i>	900.0	189	0.041	surface	MONTICELLI (2011)

To evaluate relationships between BW and MF or D of male mating vocalizations, two different linear regression analyses were performed. First, an ordinary least squares (OLS) regression was carried out. Although this approach allows the comparison with other studies, it fails to account for non-independence of taxa. Therefore, we secondly used a phylogenetic generalized least square (PGLS) regression implemented in the R package “caper” (ORME et al. 2013). In both cases, variables were log transformed before regression analyses.

To test whether phylogenetic relationships affect vocalization’s variables in subterranean and surface-dwelling species, we first constructed a topological phylogenetic tree. The tree was constructed by subsetting the mammal tree from [vertlife.org](https://vertlife.org) website (<https://vertlife.org/phylosubsets>; UPHAM et al. 2019). We downloaded 100 pseudo-posterior distribution trees, which were used to produce a single maximum clade credibility (MCC) tree (Fig. 1) using the TreeAnnotator utility (RAMBAUT et al. 2018) in BEAST (DRUMMOND & RAMBAUT 2007). To assess the amount of phylogenetic signal for MF, D and BW, that is, the extent to which closely related species tend to resemble each other (BLOMBERG et al. 2003, SYMONDS

& BLOMBERG 2014), Pagel’s lambda parameter ( $\lambda$ ) was chosen (PAGEL 1999). Pagel’s  $\lambda$  is one of the most commonly used quantitative measures of phylogenetic signal (SYMONDS & BLOMBERG 2014). Values vary from zero (independence from phylogeny) to 1 (indicating that traits among related species are more similar than expected as the result of phylogeny). This analysis was performed with the function “phylosig” R package “phytools” (REVELL 2012). To evaluate if MF and D differ among rodents with different lifestyle, we carried phylogenetic ANOVAs to compare vocalization variables of subterranean rodents (fossorial species included) to that of surface-dwelling rodents. Analyses were run using “caper” package (ORME et al. 2018) and “ape” (PARADIS et al. 2004) packages developed in R (R Core Team 2018). Normality of the residuals was checked through a qq-plot (MUNDRY 2014).

## RESULTS

Ordinary least square regressions showed significant negative relationships between BW and MF for both subterranean and surface-dwelling rodent species, although log BW explained more than twice as much of the variance of log MF in aboveground species than in subterranean ones (subterranean:  $Y = -0.68X + 4.47$ ,  $R^2 = 0.22$ ; surface:  $Y = -1.52X + 7.09$ ,  $R^2 = 0.75$ ,  $p = 0.01$ ; Fig. 2A). Regarding log BW and logD, no relationship among both variables was found in neither subterranean nor aboveground rodents (subterranean:  $Y = -0.24X - 0.74$ ,  $R^2 = 0.04$ ; surface:  $Y = 0.06X - 1.3$ ,  $R^2 = 0.003$ ,  $p > 0.05$ ; Fig. 2B).

Regarding the phylogenetic analysis, BW, MF and D were significantly influenced by phylogeny, with  $\lambda$  values close to 1 (BW: 0.80,  $p = 0.005$ , MF: 0.78,  $p = 0.008$ , D: 0.70,  $p = 0.02$ ). Phylogenetic analyses displayed differences in MF between subterranean and surface-dwelling rodent species (Phylogenetic ANOVA,  $F = 8.26$ ,  $DF = 24$ ,  $P = 0.03$ ), while no differences were registered for D among both groups (Phylogenetic ANOVA,  $F = 0.55$ ,  $DF = 22$ ,  $P = 0.91$ ). Similar to the results of OLS, phylogenetic regressions for subterranean and surface-dwelling rodents exhibit negative relationships between BW and MF with different slopes (subterranean:  $Y = -0.62X + 4.34$ ,  $R^2 = 0.62$ ,  $p = 0.006$ ; surface:  $Y = -0.77X + 5.42$ ,  $R^2 = 0.30$ ,  $p = 0.02$ ).

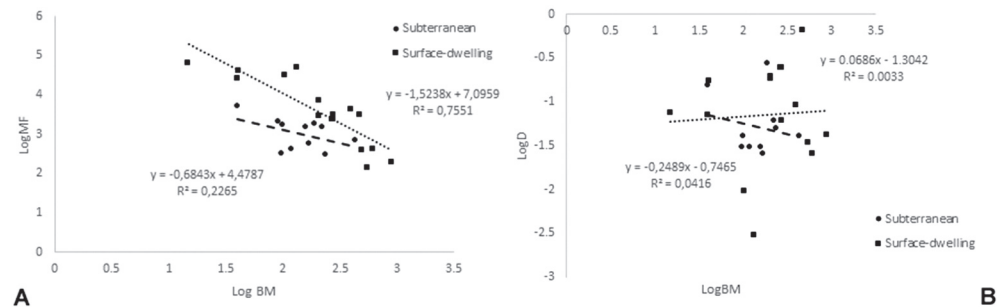


Fig. 2. A – body weight and dominant frequency of male mating calls. The base-10 logarithm of mean body weight plotted against the base-10 logarithm of mean dominant frequency. Lines depict ordinary least squares (OLS) regression. B – body weight and duration of male mating calls. The base-10 logarithm of mean body weight plotted against the base-10 logarithm of mean dominant frequency. Lines depict ordinary least squares (OLS) regression.

## DISCUSSION

Our test of morphological constraint hypothesis revealed that both groups of rodents, surface dwelling as well as subterranean, follow a negative acoustic allometry for size and frequency. Our findings are in accordance with a previous study on acoustic allometry of rodents' alarm calls (GARCÍA-NAVAZ & BLUMSTEIN 2016), as well as the study of various mammalian species (CHARLTON & REBY 2016, BOWLING et al. 2017). Although the acoustic allometry in general seems to be an universal rule, the relationship between body size and vocalization frequencies can be of different strengths e.g., carnivores perform weaker relationship than primates. The weaker size-frequency allometry in carnivores might reflect ecological differences or more frequent occurrence of non-tonal vocalizations (BOWLING et al. 2017). In the present study, the phylogenetic analysis revealed that body size explained more variation of MF in subterranean rodents than in surface-dwelling ones, suggesting that more diverse ecological factors may operate in determining acoustic parameters of vocalizations in aboveground environments compared to the more stable and uniform subterranean niche. Also, and as suggested by BOWLING et al. (2017) for carnivores, it is possible that aboveground species display a greater variability in their vocal behaviour, a situation not evaluated in this work. Interestingly, and unlike the majority of studies that restrict their analysis to alarm calls, this pattern of negative size-frequency acoustic allometry was observed in a mating call, indicating that morphological properties of the caller can influence various types of vocalizations, irrespective of their function or tonal characteristics.

Besides the observed morphological constraints, our analysis showed that conditions for acoustic propagation in the habitats of the studied subterranean and aboveground rodent species affected the evolution of MF of male mating calls. As a general pattern, subterranean rodents use lower frequency vocalizations than surface ones, a situation particularly evident in smaller species, providing support for the existence of an acoustic adaptation in subterranean rodents. Although the evidence supporting the hypothesis is scarce, one of the possible explanations for this limited proof of environmental effect on vocalization design could be the lack of highly contrasting acoustic habitats in various studies (EY & FISHER 2009, HARDT & BENEDICT 2020, MIKULA et al. 2021). Moreover, the animals are able to adjust other parameters of vocal calls like amplitude, to overcome the environmental limitations in closed habitats (CHARLTON et al. 2019). In contrast, we compared above-ground habitats with subterranean tunnels, and in the latter the transmission of high-frequency sounds is significantly limited, as explained earlier (HETH et al. 1986, LANGE et al. 2007, SCHLEICH & ANTENUCCI 2009). Apart from this physical constraint, the need for small animals to hear high frequencies in order to use binaural spectral differences is useless in the unidimensional burrows, where its sides consist of soil which do not transmit the sound and the back is mostly shielded by the body of the animal. Therefore, they do not need to use high frequencies to localize the source of sound and are limited only by ability to produce low frequency vocalizations (NARINS et al. 1992, HEFFNER & HEFFNER 2007).

The assumption of a positive influence of the body size and the lung volume on the call duration was not proved for the studied species of rodents (Fig. 2B). The call duration is influenced by other variables like call type (agonistic calls are of longer duration compared to distress calls), sex (longer calls in larger sex) and age (adults have longer calls than infants) (review in EY et al. 2007). Our study should not be influenced by those variables as we are comparing one type of the vocal signal produced by adults of one sex. The call duration is also influenced by arousal level, but it does not show a consistency across animal species. The dependency of body size on call duration was formerly studied only in individuals of one species with mixed results (HAMMERSCHMIDT et al. 2000). The single mating call duration might not be the best

proxy for the body size as the calls are quite short (0.0095–0.18 s) and often produced in bouts. It would be better to use duration of the bouts, where volume of the lungs can play a bigger role. However, this information is often lacking in published vocal repertoires.

In conclusion, the present study shows that, besides the effect of body size, acoustic differences in terms of transmission properties between subterranean and aboveground habitats also exert selective pressures on the frequency characteristic of rodent vocalizations, particularly on subterranean species. Future studies, including more subterranean and aboveground species, and precise information on the acoustic properties of the diverse aboveground habitats inhabited by surface-dwelling rodents, are needed to provide more evidence of the role of acoustic environments in the evolution of acoustic structure in animal vocalizations.

## A c k n o w l e d g e m e n t s

We would like to thank Hynek BURDA for introducing us into the world of subterranean rodents' bioacoustics and in the community of subterranean rodents' researchers. His lectures were a great inspiration for our future work and it should be noted that co-authors of this article met for the first time in his lab in Essen about 20 years ago. So Hynek, thank you.

## REFERENCES

- AHONEN H., HARCOURT R. G., STOW A. J. & CHARRIER I., 2018: Geographic vocal variation and perceptual discrimination abilities in male Australian sea lions. *Animal Cognition*, **21**: 235–243.
- AMAYA J., 2016: *Interacciones acústicas de una especie de Ctenomys de la provincia de La Rioja*. Unpubl. PhD Thesis. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, 111 pp.
- BARKER A. J., KOCH U., LEWIN G. R. & PYOTT S. J., 2021: Hearing and vocalizations in the naked mole-rat. Pp. 157–195. In: BUFFENSTEIN R., PARK T. J. & HOLMES M. M. (ed.): *The Extraordinary Biology of the Naked Mole-Rat*. Springer, Cham, 445 pp.
- BARTL J., 2006: *Lautäußerungen der Chinchillas im Sozialverband*. Unpubl. Thesis. Ludwig-Maximilians-Universität München, München, 404 pp.
- BEDNÁŘOVÁ R., HROUZKOVÁ-KNOTKOVÁ E., BURDA H., SEDLÁČEK F. & ŠUMBERA R., 2012: Vocalizations of the giant mole-rat (*Fukomys mechowii*), a subterranean rodent with the richest vocal repertoire. *Bioacoustics*, **22**: 87–107.
- BLOMBERG S. P., GARLAND T. JR. & IVES A. R., 2003: Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**: 717–745.
- BOWLING D., GARCIA M., DUNN J., RUPRECHT R., STEWART A., FROMMOLT K. H. & FITCH W. T., 2017: Body size and vocalization in primates and carnivores. *Scientific Reports*, **7**(41070): 1–11.
- BRADBURY J. W. & VEHRENCAMP S. L., 2011: *Principles of Animal Communication*. Sinauer Associates Inc., Sunderland, 882 pp.
- BRIIGGS J. R. & KALCOUNIS-RUEPPELL M. C., 2011: Similar acoustic structure and behavioural context of vocalizations produced by male and female California mice in the wild. *Animal Behaviour*, **82**: 1263–1273.
- BROOKS R. J. & BANKS E., 1973: Behavioural biology of the collared lemming: an analysis of acoustic communication. *Animal Behaviour Monographs*, **6**: 1–83.
- BRUMM H. & NAGUIB M., 2009: Environmental acoustics and the evolution of bird song. *Advances in the Study of Behavior*, **40**: 1–33.
- CAMPBELL P., PASCH B., PINO J. L., CRINO O. L., PHILLIPS M. & PHELPS S. M., 2010: Geographic variation in the songs of neotropical singing mice: testing the relative importance of drift and local adaptation. *Evolution: International Journal of Organic Evolution*, **64**(7): 1955–1972.

- CHARLTON B. D., OWEN M. A. & SWAISGOOD R. R., 2019: Coevolution of vocal signal characteristics and hearing sensitivity in forest mammals. *Nature Communications*, **10**(1): 1–7.
- CREDNER S., BURDA H. & LUESCHER F., 1997: Acoustic communication underground: vocalization characteristics in subterranean social mole-rats (*Cryptomys* sp., Bathyergidae). *Journal of Comparative Physiology A*, **180**: 245–255.
- DEVRIES S. & SIKES R., 2008: Vocalisations of a North American subterranean rodent *Geomys breviceps*. *Bioacoustics*, **18**: 1–15.
- DRUMMOND A. J. & RAMBAUT A., 2007: BEAST: Bayesian evolutionary analysis by sampling trees. *BioMedCentral Evolutionary Biology*, **7**: 214.
- DVOŘÁKOVÁ V., HROUZKOVÁ E., & ŠUMBERA R., 2016: Vocal repertoire of the social Mashona mole-rat (*Fukomys darlingi*) and how it compares with other mole-rats. *Bioacoustics*, **25**: 253–266.
- EY E. & FISCHER J., 2009: The “acoustic adaptation hypothesis” – a review of the evidence from birds, anurans and mammals. *Bioacoustics*, **19**: 21–48.
- EY E., PFEFFERLE D. & FISCHER J., 2007: Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. *Primates*, **48**: 253–267.
- FITCH W. T. & HAUSER M. D., 1995: Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on “honest” advertisement. *American Journal of Primatology*, **37**: 191–219.
- FITCH W. T. & HAUSER M. D., 2002: Unpacking “honesty”: vertebrate vocal production and the evolution of acoustic signals. Pp. 65–137. In: SIMMONS A. M., FAY R. R. & POPPER A. N. (eds.): *Springer Handbook of Auditory Research, Volume 16*. Springer, New York, 404 pp.
- FITCH T. W. & REBY D., 2001: The descended larynx is not uniquely human. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **268**: 1669–1675.
- FLOODY O. R. & PFAFF D. W., 1977: Communication among hamsters by high-frequency acoustic signals: I. Physical characteristics of hamster calls. *Journal of Comparative and Physiological Psychology*, **91**: 794–806.
- GARCÍA-NAVAS V. & BLUMSTEIN D. T., 2016: The effect of body size and habitat on the evolution of alarm vocalizations in rodents. *Biological Journal of the Linnean Society*, **118**: 745–751.
- GILLOOLY J. F. & OPHIR A. G., 2010: The energetic basis of acoustic communication. *Proceedings of the Royal Society B: Biological Sciences*, **277**: 1325–1331.
- GOURBAL B. E. F., BARTHELEMY M., PETIT G. & GABRION C., 2004: Spectrographic analysis of the ultrasonic vocalisations of adult male and female BALB/c mice. *Naturwissenschaften*, **91**: 381–385.
- HAMMERSCHMIDT K., NEWMAN J. D., CHAMPOUX M. & SUOMI S. J., 2000: Changes in rhesus macaque ‘coo’ vocalizations during early development. *Ethology*, **106**: 873–886.
- HANSEN P., 1979: Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behaviour*, **27**: 1270–1271.
- HARDT B. & BENEDICT L., 2020: Can you hear me now? A review of signal transmission and experimental evidence for the acoustic adaptation hypothesis. *Bioacoustics*, **30**(6): 1–27.
- HEFFNER R. S. & HEFFNER H. E., 1993: Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*), with an overview of central auditory structures. *Journal of Comparative Neurology*, **331**: 418–433.
- 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.
- KNOTKOVÁ E., VEITL S., ŠUMBERA R., SEDLÁČEK F. & BURDA H., 2009: Vocalizations of the silvery mole-rat: comparison of vocal repertoires in subterranean rodents with different social systems. *Bioacoustics*, **18**: 241–257.
- LANGE S., BURDA H., WEGNER R. E., DAMMANN P., BEGALL S. & KAWALIKA M., 2007: Living in a “stethoscope”: burrow-acoustics promote auditory specializations in subterranean rodents. *Naturwissenschaften*, **94**: 134–138.
- LIEBERMAN P., 1984: *The Biology and Evolution of Language*. Harvard University Press, Cambridge, 392 pp.
- MANNO G. T., NESTEROVA A. P., DEBARBIERI L. M., KENNEDY S. E., WRIGHT K. S. & DOBSON S., 2007: Why do male Columbian ground squirrels give a mating call? *Animal Behavior*, **74**: 1319–1327.



- MARTEN K. & MARLER P., 1977: Sound transmission and its significance for animal vocalization. I. Temperate habitats. *Behavioral Ecology and Sociobiology*, **2**: 271–290.
- McCLATCHIE S., ALSOP J. & COOMBS R.F., 1996: A re-evaluation of relationships between fish size, acoustic frequency, and target strength. *International Council for the Exploration of the Sea Journal of Marine Science*, **53**: 780–791.
- MIKULA P., VALCU M., BRUMM H., BULLA M., FORSTMEIER W., PETRUSKOVÁ T., KEMPENAERS B. & ALBRECHT T., 2021: A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. *Ecology Letters*, **24**: 477–486.
- MONTICELLI P., 2011: *Aspectos acústicos da domesticação: os chamados de corte e alerta no preá cavia apereae na cobaia cavia porcellus*. Unpubl. MSc. Thesis. Sao Pablo University, Sao Pablo, 81 pp.
- MORTON E. S., 1975: Ecological sources of selection on avian sounds. *American Naturalist*, **109**: 17–34.
- MUNDURY R., 2014. Statistical issues and assumptions of phylogenetic generalized least squares. Pp. 131–153. In: GARAMSZEI L. Z. (ed.): *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. Springer-Verlag, Berlin & Heidelberg, 552 pp.
- ORME D., FRECKLETON R. P., THOMAS SHOW G. H., PETZOLDT T., FRITZ S. A. & ISAAC N. J. B., 2013: CAPER: comparative analyses of phylogenetics and evolution in R. *Methods in Ecology and Evolution*, **3**: 145–151.
- PADGHAM M., 2004: Reverberation and frequency attenuation in forests – implications for acoustic communication in animals. *Journal of the Acoustical Society of America*, **115**: 402–410.
- PAGEL M., 1999: Inferring the historical patterns of biological evolution. *Nature*, **401**(6756): 877–884.
- PARADIS E., CLAUDE J. & STRIMMER K., 2004: APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics*, **20**: 289–290.
- PEARSE W. D., MORALES-CASTILLA I., JAMES L. S., FARRELL M., BOIVIN F. & DAVIES T. J., 2018: Global macroevolution and macroecology of passerine song. *Evolution*, **72**: 944–960.
- PEPPER J. W., BRAUDE S. H., LACEY E. A. & SHERMAN P. W., 1991: Vocalizations of the naked mole-rat. Pp. 243–274. In: SHERMAN P. W., JARVIS J. U. M. & ALEXANDER R. D. (eds.): *The Biology of the Naked Mole-rat*. Princeton University Press, Princeton, 536 pp.
- PUECHMAILLE S. J., GOUILH M. A., PIYAPAN P., YOKUBOL M., MIE K. M., BATES P. J., SATASOOK C., NWE T., HLA BU S. S., MACKIE I. J., PETIT E. J. & TEELING E. C., 2011: The evolution of sensory divergence in the context of limited gene flow in the bumblebee bat. *Nature Communications*, **2**(573): 1–9.
- RAMBAUT A., DRUMMOND A. J., XIE D., BAELE G. & SUCHARD M. A., 2018: Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, **67**: 901–904.
- REVELL L. J., 2012: phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **2**: 217–223.
- RICHARDS D. G. & WILEY R. H., 1980: Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *American Naturalist*, **115**: 381–399.
- RYAN M. J. & BRENOWITZ E. A., 1985: The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist*, **126**: 87–100.
- SCHLEICH C. E. & ANTENUCCI D. C., 2009: Sound transmission and burrow characteristics of the subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae). *Acta Theriologica*, **54**: 165–170.
- SCHLEICH C. E. & BUSCH C., 2002: Acoustic signals of a solitary subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae): Physical characteristics and behavioural correlates. *Journal of Ethology*, **20**: 123–131.
- SYMONDS M. R. E. & BLOMBERG S. P., 2014: A primer on phylogenetic generalised least squares. Pp. 105–130. In: GARAMSZEI L. Z. (ed.): *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. Springer-Verlag, Berlin, 552 pp.
- TAMURA N., 1993: Role of sound communication in mating of Malaysian *Callosciurus* (Sciuridae). *Journal of Mammalogy*, **74**: 468–476.
- TAMURA N., BOONKHAW P., PRAYOON U., KANCHANASAKA B. & HAYASHI F., 2018: Mating calls are a sensitive indicator of phylogenetic relationships in tropical tree squirrels (*Callosciurus* spp.). *Mammalian Biology*, **93**: 198–206.

- TAYLOR A. M. & REBY D., 2010: The contribution of source-filter theory to mammal vocal communication research. *Journal of Zoology, London*, **280**: 221–236.
- VANDEN HOLE C., VAN DAELE P. A. A. G., DESMET N., DEVOS P. & ADRIAENS D., 2014: Does sociality imply a complex vocal communication system? A case study for *Fukomys micklemi* (Bathyergidae, Rodentia). *Bioacoustics*, **23**: 143–160.
- VEITL S., BEGALL S. & BURDA H., 2000: Ecological determinants of vocalisation parameters: the case of the coruro *Spalacopus cyanus* (Octodontidae), a fossorial social rodent. *Bioacoustics*, **11**: 129–148.
- VERZOLA-OLIVIO P. & MONTICELLI P., 2017: The acoustic repertoire of *Cavia intermedia* as a contribution to the understanding of the Caviidae communication system. *Bioacoustics*, **26**: 285–304.
- WALLSCHLÄGER D., 1980: Correlation of song frequency and body weight in passerine birds. *Experientia*, **36**: 412.
- WHITE N. R., CAGGIANO R., MOISES A. U. & BARFIELD R. J., 1990: Changes in Mating Vocalizations Over the Ejaculatory Series in Rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, **3**: 255–262.
- WILEY H. R. & RICHARDS D. G., 1982: Adaptations for acoustic communication in birds: sound transmission and signal detection. Pp. 131–181. In: KROODSMA D. E. & MILLER E. H (eds.): *Acoustic Communication in Birds*. Academic Press, New York, 371 pp.