**ORIGINAL ARTICLE**

# Locomotion and postures of the Vietnamese pygmy dormouse *Typhlomys chapensis* (Platacanthomyidae, Rodentia): climbing and leaping in the blind

Dionisios Youlatos[1] · Aleksandra A. Panyutina[2] · Makrina Tsinoglou[1] · Ilya A. Volodin[3]

## Abstract

The Vietnamese pygmy dormouse is a small, arboreal, nocturnal, blind rodent that uses incipient echolocation to navigate in tree canopies. In order to assess its arboreal faculties in relation to echolocative capacity, the present study investigated the locomotor and postural behavior of the species in a simulated arboreal environment within an enclosure. The study subjects were intensively video and audio recorded and the two sets of data were synchronized for subsequent analyses. This is the first study on the positional behavior and substrate use of the Vietnamese pygmy dormice. Our results showed that the species spent most of its time on arboreal substrates, mostly traveling and scanning. Locomotion was dominated by vertical climb and leap, occurring mostly on small vertical and on medium and large strongly inclined substrates, respectively. Locomotion and substrate type were strongly related to emission of echolocative pulses. These findings most likely suggest that echolocation compensates for poor vision to effectively negotiate highly challenging arboreal constraints, and are in favor of the arboreal origins of pygmy dormice. Moreover, such a scenario could also support the echolocation-first hypothesis for the emergence of echolocation in bats prior to active flight.

**Keywords** Locomotion · Postures · Echolocation · Arboreal · Non-visual orientation

## Introduction

The enigmatic rodent family Platacanthomyidae is the earliest phylogenetic offshoot of the Muroidea and includes two morphologically unique genera distributed in the highlands of South and Southeast Asia (Musser and Carleton 2005; Lv et al. 2006; Jansa et al. 2009): the monotypic Malabar spiny dormouse *Platacanthomys*, restricted to the mountains of south-western India, and the pygmy dormouse *Typhlomys*, confined to the highlands of southern China and northern Vietnam (Wilson and Reeder 2005). Recent research has

shown that the genus *Typhlomys* includes four species: *Typhlomys cinereus, T. daloushanensis,* and *T. nanus* are endemic to China, while *T. chapensis* is found in southern China and northern Vietnam (Wu and Wang, 1984; Wang et al. 1996; Cong et al. 2013; Abramov et al. 2014; Cheng et al. 2017). The Chapa or Vietnamese pygmy dormouse *Typhlomys chapensis* Osgood, 1932 is a nocturnal small rodent (body mass about 10–20 g, head-body length about 70–100 mm), with yellowish gray soft dorsal pelage and slate gray ventral pelage, with a particularly long hairy tail (length about 100–135 mm), and prominent ears (length about 14–19 mm) (Abramov et al. 2014; Cheng et al. 2017). It bears very small, reduced eyes, with an inner morphology that shows a significant structural degradation and suggests the loss of visual acuity and focus (Panuytina et al. 2017; Volodin et al. 2019). Such an organ is only suited for distinguishing dark from light or help photoperiodicity, justifying its generic name meaning 'blind mouse' (Panuytina et al. 2017; Volodin et al. 2019). Moreover, *T. chapensis* is characterized by regression of the gene for the interphotoreceptor retinoid-binding protein (IRBP), which plays an important role in the visual cycle (Cheng et al. 2017), as in

Handling editor: Daisuke Koyabu.

✉ Dionisios Youlatos
  dyoul@bio.auth.gr

1 Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece

2 Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

3 Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia

subterranean mammals, such as mole-rats, golden moles, and true moles (Emerling and Springer 2014).

On the other hand, the species has developed a unique system of ultrasonic echolocation for beyond-tactile orientation during locomotion (Panyutina et al. 2017; Volodin et al. 2019). The ultrasonic vocalization of *Typhlomys* is reminiscent of bat echolocation calls, yet the sweeps in this rodent are faint, compared to those of bats (Panyutina et al. 2017; Volodin et al. 2019). This unique adaptive mechanism appears to facilitate arboreal faculties, including confident progression through an unfamiliar environment, over inclined and vertical branches, as well as aimed leaps from branch to branch, over gaps several times greater than the tactile reach of the vibrissae (Panyutina et al. 2017). This lifestyle of *Typhlomys* is also implied by the long vibrissae, large ears, long hind feet and elongated hairy tail, although there is little direct evidence on its biology (Abramov et al. 2014; Panyutina et al. 2017). Similar morphological adaptations are also found in some other nocturnal rodents, but, in contrast to *Typhlomys,* they are coupled with relatively large specialized eyes (Cartmill 1985; Niederschuh et al. 2015, 2017; Arkley et al. 2017). In fact, the incipient echolocation of *Typhlomys* is very likely a compensatory mechanism for the poor vision and focus for canopy exploration (Panyutina et al. 2017). This interplay between echolocation and arboreal exploration may have important implications for understanding the evolution of non-visual orientation and, more particularly, echolocation in bats (Fenton et al. 1995; Jones and Teeling 2006; Teeling et al. 2012; Carter and Adams 2015, 2016; Adams and Carter 2017; Panuytina et al. 2017).

In order to assess the arboreal faculties of the Vietnamese pygmy dormice, the present study investigated the locomotor and postural behavior of the species in a simulated arboreal environment within an enclosure. The arboreal environment is a three-dimensional discontinuous network of unstable, structurally variable and diversely oriented substrates. To move rapidly along arboreal substrates, to climb up or down vertical substrates, and to cross wide gaps represent the most demanding locomotor challenges within the arboreal environment (Cartmill 1985). In the case of a scansorial mammal, such as *Typhlomys*, the poor eyesight and ill focus would significantly reduce the efficiency of balance on small unstable substrates, the secure use of steeply inclined substrates, and the successful negotiation of wide gaps between substrates. Extensive use of relatively wide and horizontal substrates and the crossing of small gaps, where the tactile vibrissae would serve as guide, would be more suitable. However, if the echolocative capacity of *Typhlomys chapensis* allows for successful canopy orientation, we expect this species (a) to exhibit an agile arboreal repertoire, (b) to frequently use vertical climbing and leaping, and (c) to prefer and commonly use small unstable and strongly inclined arboreal substrates.

## Materials and methods

### Studied subjects

For the purposes of the current study, we observed and filmed two male Chapa pygmy dormice *Typhlomys chapensis* (Rodentia, Muroidea, Platacanthomyidae). The two studied animals were collected in mountain tropical forest in northern Vietnam between 2010–2012 by live cagetraps set up on branches and on the ground (Panyutina et al. 2017). The two animals were kept at the Moscow Zoo in relatively large and enriched cages, where they could move on different kinds of substrates and on the cage floor. Both males were fully habituated to human presence, and did not display any stereotypical or stressful behaviors at the time of the observations. Although the number of the sampled individuals is limited, it is important to note that the animal is classified as endangered, it has a restricted range, is rare and difficult to catch in the field. Furthermore, the studied individuals are the only ones kept alive in a zoo in the world underlining the paramount importance of behavioral observations.

### Video and audio recordings

The present data derived from the analysis of video recordings of the two captive males. Video recording for behavioral observation occurred in a specific experimental enclosure (height: 50 cm × length: 120 cm × depth: 30 cm) backed by white plastic walls, fronted by a glass window, with wiremesh sides. The floor was covered with mulch. Within the enclosure, a variety of arboreal substrates of various sizes and inclinations were arranged enabling the animals to move freely. The recording sessions occurred between February and July 2013. Two camcorders were applied simultaneously for video recording: a JVC GC-PX10 camcorder (Victor Company of Japan, Yokohama, Japan) was used for the high-definition video (1920 × 1080 pixels, 50 fps, 1/1000 s) and a Casio EX-F1 camcorder (Casio Computer, Tokyo, Japan) was used for the high-speed video (512 × 384 pixels, 299.7 fps, 1/2000s). The total duration of the analyzed videos was 106.6 min. The experiments are described in detail in Panyutina et al. (2017).

During the video recording procedures, a Pettersson D 1000X recorder with a built-in microphone (Pettersson Elektronik AB, Uppsala, Sweden) was used for the audio recording (sampling rate 768 kHz, 16 bit; frequency response from 5 to 235 kHz). The total duration of the audio recordings accompanying the videos was 60.6 min. The respective audio- and video-tracks were synchronized based on clicker signals.

The present research followed the guidelines for the treatment of animals in behavioral research and teaching (ASAB/ABS 2020) and was approved by the Committee of Bioethics of the Lomonosov Moscow State University (research protocol no. 2011-36).

## Behavioral data collection and analysis

Available substrates in an artificial enclosure are expected to limit positional options of animals and, therefore, an estimate of their availability would allow for a controlled test of substrate preference or avoidance. The size and inclination of all available substrates were calculated by unit, and subsequently, we estimated the availability of the different size and inclination categories (see Table 1 for definitions and descriptions). Regarding size, medium-sized substrates prevailed (small: 37%, medium: 44%, large: 19%). In terms of inclination, oblique substrates were the most available (horizontal: 14%, oblique: 55%, vertical: 31%). Then, preference or avoidance of these categories was estimated by

Jacobs' $D$ value $D = U - A/U + A - 2U \times A$, where $U$ is proportion of use, and $A$ is proportion of availability (Jacobs 1974). Values of the index range from $-1$, indicating strong avoidance, to $+1$, showing strong preference, whereas values around 0 are considered as neutral.

During video analysis, we used the focal animal bout sampling method (Martin and Bateson 1993) to collect the following variables: (a) behavioral context, (b) substrate type, (c) substrate size, (d) substrate inclination, and (e) locomotor/postural mode (see Table 1 for definition of the different categories of the variables). Substrate size was determined by the capacity of full or partial pedal grasp and substrate inclination categories followed those of previous studies (e.g., Youlatos et al. 2015). Although the bout method does not guarantee the independence of behavioral events, it is most suitable for small, fast and agile mammals, as it can capture their behavioral diversity through the recording of rare or occasional events. During data collection, a bout ended when one of the recorded variables changed. To address the shortcoming of autocorrelation of

**Table 1** Definition and description of the recorded variables for captive *Typhlomys chapensis*

| Behavioral context | | |
|---|---|---|
| Travel | LC | Body displacement |
| Scan | SC | Inspecting and exploring the surroundings |
| Rest | RE | Short or long periods of inactivity |
| Burrow | BR | Digging and burrowing in the mulch of the cage floor |
| Groom | GR | Body and fur maintenance and cleaning |
| Substrate size | | |
| Small | S | Substrate that can be fully grasped by foot |
| Medium | M | Substrate that can be only partly grasped by foot |
| Large | L | Substrate that cannot be grasped by foot |
| Substrate inclination | | |
| Horizontal | H | Angle between 0°–22.5° |
| Oblique | O | Angle between 22.5°–67.5° |
| Vertical | V | Angle between 67.5°–90° |
| Locomotor modes | | |
| Quadrupedalism | QD | Symmetrical slow or moderate (walk), symmetrical fast (run) and asymmetrical fast (bound) progression along single horizontal and moderately inclined substrates |
| Vertical climb | VC | Symmetrical quadrupedal or asymmetrical bounding ascent or descent along vertical or steep substrates |
| Clamber | CL | Irregular pronograde or semipronograde quadrupedal locomotion across multiple substrates, sometimes over small gaps |
| Leap | LP | Gap crossing mode involving an airborne phase with the body held horizontally or inclined, directed upwards, horizontally, or downwards, also involving hopping |
| Reversion | RV | Instantaneous 180° switch of direction on vertical substrates involving an aerial phase with no height loss |
| Postural modes | | |
| Stand | ST | Pronograde quadrupedal posture with either strongly flexed or semi-extended limbs |
| Sit | SI | Orthograde or leaning seated posture with strongly flexed hind limbs |
| Cling | CG | Orthograde gripped posture with extremely flexed limbs and the head upwards or downwards on vertical or steep substrates |
| Cantilever | CA | Grasping feet secure the lower part of the body to a substrate while the trunk and forelimbs are extended horizontally |
| Hang | HG | Suspensory posture below a substrate using all four limbs or using the hind limbs only |

successive sampling events, we followed a trimming procedure as in previous studies (e.g., Youlatos et al. 2015). Initially, each complete dataset for each individual was divided into the locomotor and postural subsets. Then, in each subset, we only considered every second bout ($b$, $b+2$), deleting each intermediate one ($b+1$). Following this trimming procedure, we calculated the frequencies of substrate type, size, and inclination use and the frequencies of locomotor and postural modes for each individual. These frequencies were statistically compared using chi-squared test and no differences were detected between the two sampled individuals (Mehta and Patel 1995). Subsequently, all data subsamples were grouped together, totaling to 1506 bouts of locomotion and 1744 bouts of postures, for further analyses. Differences among frequencies of behaviors or substrate use were calculated using log-likelihood ratio $G$ tests (Mehta and Patel 1995).

## Acoustic activity analysis

For the acoustic analysis, the audio recordings were sampled by selecting the first half-second fragment from every 5-s interval. Audio track was explored with Syrinx software (https://www.syrinxpc.com/). The number of the ultrasonic pulses emitted by animals was counted for each half-second fragment and recalculated into the pulse rate, which is the number of pulses per second (Volodin et al. 2019). Behavioral activity was classified for each selected half-second fragment by viewing the video track. In contrast to the complete behavioral analysis described above, for the acoustic analysis we considered only (a) behavioral context, (b) locomotor activity (locomotion/posture), and (c) substrate type. In total, 553 half-second fragments were analyzed. For all these parameters the pulse rate was used as an estimate of the ultrasonic activity. In order to assess how adaptation to the experimental enclosure affects the rate of emission of the ultrasonic pulses (pulse rate), we assigned a time rank for all intervals of 5 s during one day of recording, which in fact represents the number of the second during the whole experiment (1: the first interval of shooting, $1+5=6$: the second interval, etc.). All pauses between videos were also taken into account, i.e. after an hour break in the shooting, the first interval of the next shooting received a rank of $+3600$ to the last interval of the previous shooting, etc.

We used the open-source R software environment for statistical computing and graphics (version 3.5.0 and 3.5.3) under an integrated development environment for R—RStudio 295 (RStudio Desktop version 1.1.447 and 1.1.463) for the analysis of the acoustic data. We used the generalized linear regression (glm function in R) and random forest algorithm (ranger package in R) (for protocol see, e.g., Grinkov et al. 2019) to find the most parsimonious models describing the relationship between the predictors (time spent in the experimental enclosure, locomotor activity, behavioral context, substrate type, day of recording, number of individuals) and the dependent variable (pulse rate). Model selection was done using likelihood ratio test (LR test) in GLM [running anova (my.mod, test = "Chisq")]. Model performance in random forest was done by calculating the root mean square prediction error (RMSE). Significance of the predictor for estimation of the dependent variable was calculated using the variable importance (the variable importance was measured as the variance of the responses). To obtain the most accurate predictions, the random forest parameters were optimized. After tuning, the random forest improved, but only a little better. The prediction error (the mean squared error, MSE) decreased from 9.39 to 9.37, while the coefficient of determination (R2, the proportion of the variance in the dependent variable that is explained by the set of predictors) increased from 48.7 to 48.9%. The Spearman's rank correlation coefficient was used to define correlation between variables. The coefficient of variation ($CV = \sigma/\bar{x}$, where $\sigma$ is standard deviation, $\bar{x}$ is mean) was used to compare variability between different measures.

## Results

### Behavioral data

During behavioral observations, Chapa pygmy dormice spent more time on 'arboreal' substrates [i.e., the branches (41.6%) and the wire mesh wall (22.5%)] than on 'terrestrial' ones (cage floor: 35.9%). Travel (46.9%) and scan (42.2%) were the dominant behaviors. Groom, rest and burrow were infrequently used. Both travel and scan occurred significantly more often than other behaviors on arboreal substrates (69.5 and 62.5%, respectively; travel vs. rest: $G = 119.4$, $P < 0.001$; travel vs. groom: $G = 47.1$, $P < 0.001$; scan vs. rest: $G = 72.3$, $P < 0.001$; scan vs. groom: $G = 47.8$, $P < 0.001$). Compared to other behaviors, scan occurred

**Table 2** Percentages of arboreal substrate size and inclination use during the main behavioral contexts of captive *Typhlomys chapensis*

|  | Travel % | Scan % | Rest% |
|---|---|---|---|
| Size |  |  |  |
| Small | 35.1 | 42.4 | 40.4 |
| Medium | 28.3 | 21.9 | 9.1 |
| Large | 36.5 | 35.7 | 50.4 |
| Inclination |  |  |  |
| Horizontal | 8.7 | 9.4 | 47.1 |
| Oblique | 45.7 | 37.7 | 8.8 |
| Vertical | 45.5 | 52.9 | 44.1 |
| $N$ | 1058 | 857 | 135 |

significantly more often on small substrates and on vertical substrates (Table 2; substrate size: scan vs. travel: $G = 14.8$, $P = 0.0008$; scan vs. rest: $G = 46.3$, $P < 0.001$; scan vs. groom: $G = 20.7$, $P < 0.001$; substrate inclination: scan vs. locomotion: $G = 12.8$, $P = 0.0017$; scan vs. rest: $G = 38.7$, $P < 0.001$; scan vs. groom: $G = 29.4$, $P < 0.001$).

For all subsequent analyses, we only considered the activities performed on branches, as we were mainly interested in understanding how the Chapa pygmy dormice negotiate arboreal substrates. Overall, both small substrates and vertical substrates were extensively used (Fig. 1). Both categories were also strongly preferred (small $D = 0.46$, vertical $D = 0.40$). There was also a weak preference for

medium-sized substrates ($D = 0.22$), whereas all other size and inclination categories were either avoided (large $D = -0.20$) or used according to availability (horizontal $D = -0.04$; oblique $D = 0.13$). During locomotor activities, small and large substrates, and oblique and vertical substrates, were equally used (Fig. 1). However, during postural behavior, there was a significant increase in the use of small and of vertical substrates (Fig. 1; size: $G = 30.5$, $P < 0.001$; inclination: $G = 22.7$, $P < 0.001$).

Vertical climb was the dominant locomotor mode (Fig. 2). The majority of these bouts consisted of symmetrical quadrupedal climbs using the claws (70.5%, $N = 459$), while the rest was vertical bounds. Climb occurred primarily



**Fig. 1** Percentages of use of substrate size and inclination by captive *Typhlomys chapensis*
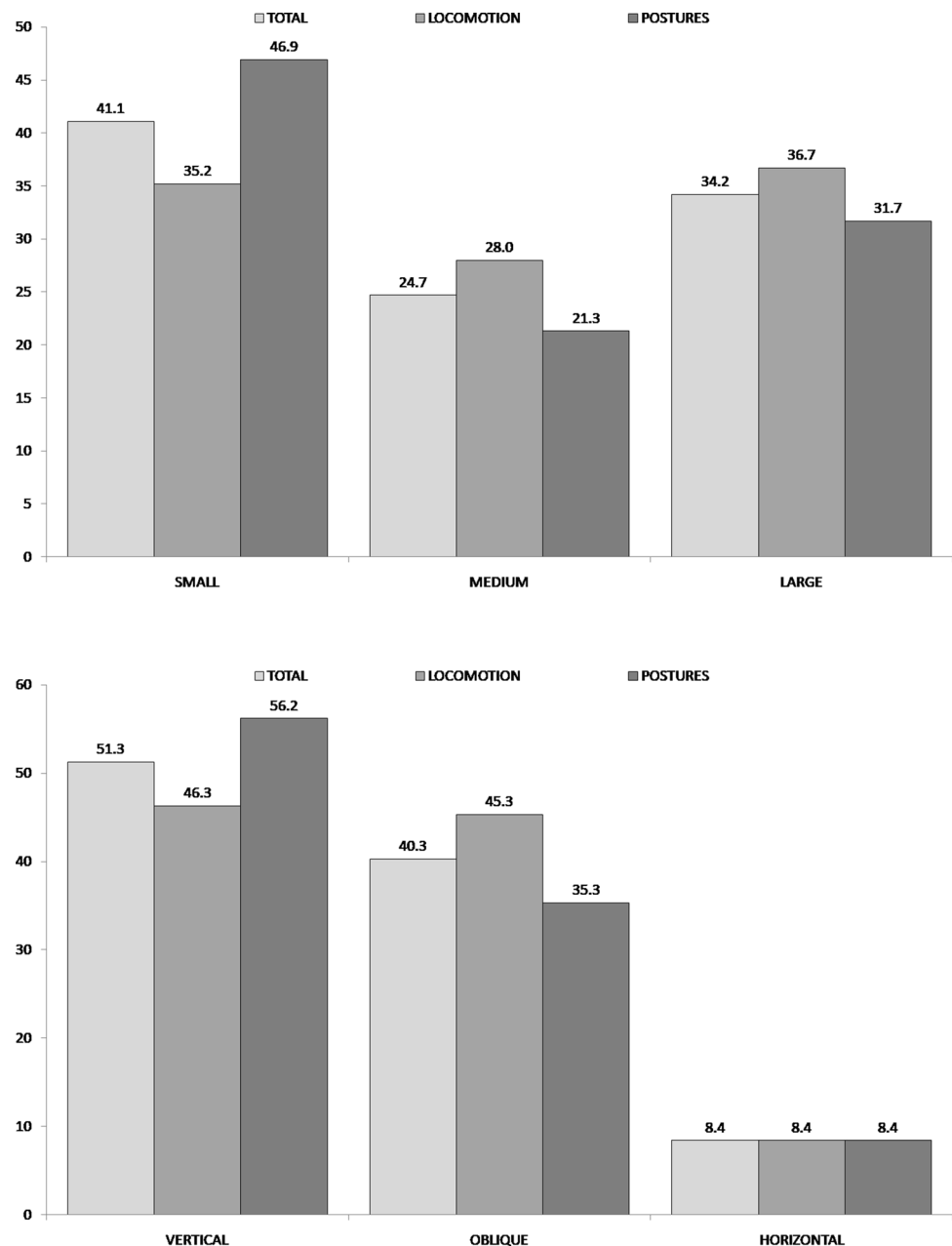
**Fig. 2** Percentages of locomotor modes (top) and postural modes (bottom) by captive *Typhlomys chapensis* (top, *VC* vertical climb, *LP* leap, *CL* clamber, *QD* quadrupedal walk, *RV* reversion; bottom, *CG* cling, *ST* stand, *HG* hang, *CA* cantilever, *SI* sit)
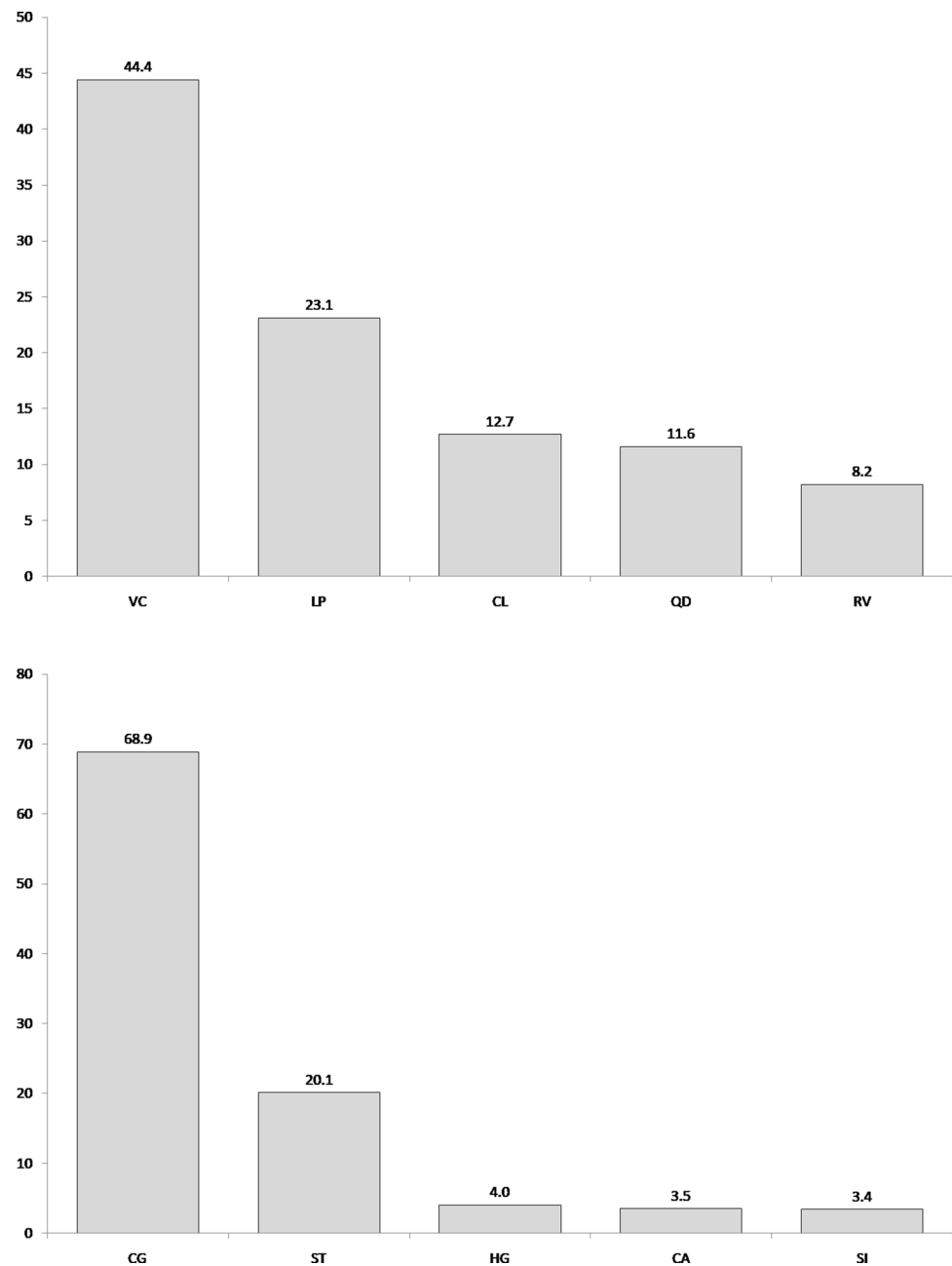


**Table 3** Percentages of arboreal substrate size and inclination use in the main locomotor and postural modes of captive *Typhlomys chapensis*

|  | Vertical climb % | Leap takeoff % | Leap land % | Clamber % | Quadrupedalism % | Cling % | Stand % |
|---|---|---|---|---|---|---|---|
| Small | 44.0 | 26.8 | 22.6 | 31.3 | 12.5 | 57.5 | 16.6 |
| Medium | 19.8 | 30.5 | 31.7 | 48.1 | 31.7 | 16.7 | 31.3 |
| Large | 36.2 | 42.7 | 45.7 | 20.6 | 55.8 | 25.8 | 52.1 |
| Horizontal | 0.0 | 12.6 | 33.9 | 10.7 | 34.2 | 0.1 | 35.1 |
| Oblique | 35.1 | 52.7 | 38.2 | 61.8 | 65.8 | 26.2 | 58.7 |
| Vertical | 64.9 | 34.7 | 27.9 | 24.5 | 0.0 | 73.7 | 6.2 |
| *N* | 459 | 239 | 239 | 131 | 120 | 722 | 211 |

on small and large vertical substrates (Table 3). Leap was the second most frequent locomotor mode (Fig. 2). Most leaps were short (< 20 cm: 67.0%, $N = 185$) or covered distances between 20–40 cm (24.9%), whereas longer leaps were occasional (8.1%). Leaps usually initiated from and terminated on large and medium substrates (Table 3; $G = 1.0$, $P = 0.623$). Regarding substrate inclination, the most frequent takeoff substrates were oblique and vertical, whereas the most frequent landing substrates were oblique and horizontal (Table 3; $G = 28.1$, $P < 0.001$). Clamber and quadrupedalism were moderately used. Medium and oblique substrates (48.1 and 61.8%, respectively, $N = 131$) dominated during clamber (Table 3), whereas large and oblique substrates were extensively used during quadrupedalism (55.8 and 64.2%, respectively, $N = 120$; clamber vs. quadrupedalism substrate size: $G = 35.9$, $P < 0.001$; substrate inclination: $G = 50.5\%$, $P < 0.001$). Reversion, i.e., a rapid switch of direction of movement, occurred primarily on small and on vertical substrates (51.7 and 69.4% respectively, $N = 85$).

In terms of postures, cling was the dominant posture (Fig. 2) and occurred principally on small and vertical substrates (Table 3). Stand was the second most frequent posture (Fig. 2) and was used primarily on large and oblique substrates (Table 3; cling vs. stand: substrate size: $G = 118.1$, $P < 0.001$; substrate inclination: $G = 443.8$, $P < 0.001$). Hang from the hind limbs, cantilever with the aid of the anchored hind limbs, and sit were used more occasionally and completed the arboreal postural profile of Chapa pygmy dormice (Fig. 2).

## Acoustic data

The acoustic analysis showed that the emission of ultrasonic calls (number of ultrasonic pulses within half-second intervals) depended on animal activity, behavioral context, and type of substrate. Activity (locomotion or posture) revealed the strongest correlation to the pulse rate (Spearman corr. $= 0.6$, $N = 553$, $P < 0.001$). During locomotion, the average ultrasonic pulse rate (number of ultrasonic pulses per second, pulse/s) was 14.3, but only 1.08 during postures. The coefficient of variation (CV) for locomotion was 1 and for postures 3.6, indicating a high variation in the pulse rate during the absence of movement.

Behavioral context also showed a relatively strong negative correlation to the ultrasonic pulse rate (Spearman corr. $= -0.49$, $N = 553$, $P < 0.001$). As Travel (behavior) corresponded to Locomotion (activity), they exhibited the same average pulse rate [14.3 pulse/s, (CV = 1)]. However, pulse rates were much lower for Burrow (3.2 pulse/s, CV = 2.5), Scan (1.2 pulse/s, CV = 3.4), Groom (1.6 pulse/s, CV = 2.5), and was zero for Rest (Fig. 3). These differences indicate that emission of pulses is high and constant during movement (travel/locomotion), but much lower to
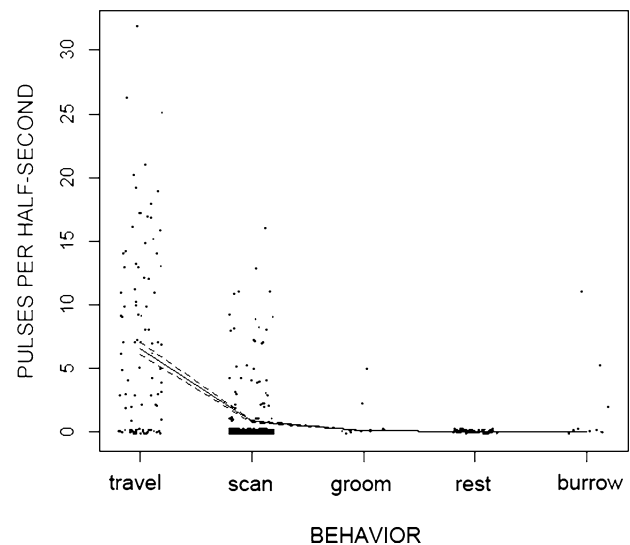


**Fig. 3** Dependencies of the number of ultrasonic pulses in a half-second interval (values equal to the half of the pulse rate as defined in the text) from behavioral context

null during other behaviors. In the latter, there were either numerous (e.g., scan) or only rare (e.g., burrow or groom) outbursts with high pulse rate. If travel is excluded from our analysis, there is no correlation between the pulse rate and the rest of the behaviors (Spearman corr. $= -0.07$, $N = 458$, $P > 0.05$).

Substrate type also affected the rate of ultrasonic pulse emission (Spearman corr. $= -0.49$, $N = 553$, $P < 0.001$). The highest pulse rate was on the floor (5.35 pulse/s, CV = 1.8) and on the branches (4.07 pulse/s, CV = 2.6), but it was much lower on the wire mesh wall (1.41 pulse/s, CV = 3.2). These scores indicate that on the wire mesh wall, although the average pulse rate was small, there were a lot of high-rate outbursts. In contrast, on the floor, the pulse rate was high and relatively constant. Lastly, when on the branches, pulse emission was high and displayed a substantial variation.

Lastly, we wanted to test which factors interrelate best to the emission of echolocation calls. Our analysis, using the random forest algorithm, showed that time rank (time spent in the experimental enclosure), locomotor activity, and behavioral context are the most important factors (Fig. 4). The importance of time spent in the experimental enclosure was further substantiated as its exclusion led to a drop in the predicting value of our model from 48.8 to 38.4%. In contrast, the exclusion of either locomotor activity or behavioral context slightly increased the predictive power of the model up to 49%. This indicates the equivalent influence of these two factors on the emission of echolocation calls, since they are highly correlated (Spearman corr. $= 0.78$, $N = 553$, $P < 0.0001$). Finally, the analysis of the impact of time spent in the experimental enclosure on the emission of ultrasonic
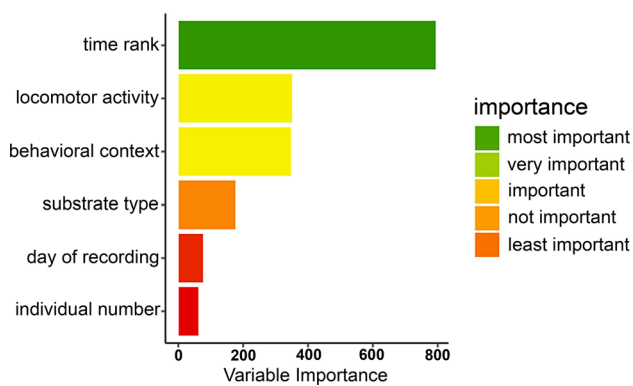
**Fig. 4** Importance of different factors for predicting the emission of echolocation calls (pulse rate), using the random forest algorithm (time rank: time spent in the experimental enclosure; locomotor activity; behavioral context; substrate type; day of recording: cumulative time since the first recording; individual number: number of studied individuals)

pulses showed the absence of a monotonic dependence (Spearman corr. = − 0.01, $P = 0.812$). This indicates that the emission of signals did not tend to change with time. Locomotor activity also showed no dependence on time (Spearman corr. = 0.03, $P = 0.5$).

## Discussion

### Locomotion, postures and substrate use

To our knowledge, this is the first study on the locomotion, postures, and substrate use of *Typhlomys chapensis*. The results strongly suggest that, in the experimental setup, *Typhlomys* is an active rodent, spending most of its time (~65%) on arboreal substrates and displaying high rates of travel and scan (~90% of time). In fact, both travel and scan occurred primarily on arboreal substrates. Regarding substrate use, *Typhlomys* used mainly the branches and secondarily the cage floor. This profile fits well with field observations indicating that individuals of this species were captured by live-traps placed on both the ground and tree branches (Abramov et al. 2014). Moreover, the substantial use of the wire mesh, in the enclosure walls, enabled *Typhlomys* to use non-pronograde positional modes and firm grasp by the extremities.

In terms of behavior, our study showed that *Typhlomys* exhibited a rather agile and diverse positional repertoire. Ultrasonic calls were primarily used during active locomotion, either on the cage floor or on the branches, but vocal activity was significantly reduced during postural behavior. Regarding locomotor behavior, climb and leap were the most frequently used modes. Quadrupedalism and clamber were used to a lesser extent. These latter modes are

important for body transfer within the arboreal milieu, but they occur along continuous or across adjacent substrates, involve a regular pattern of limb movements, and do not impose critical constraints (Fischer et al. 2002). On the other hand, climb and leap are mechanically and energetically demanding, as they both challenge gravity. The proportion of clawed vertical climbing in *Typhlomys* is comparable to that of small-sized squirrels (Youlatos 1999, 2011; Youlatos and Panyutina 2014), but very different from that of other muroid rodents, which emphasize on quadrupedalism and clamber (Urbani and Youlatos 2013; Youlatos et al. 2015). Small body size provides a better body mass to muscle force ratio (Preuschoft et al. 1998), which reduces the energetic cost (Hanna et al. 2008) providing an advantage for clawed vertical locomotion. However, small squirrels mainly claw climb on large vertical substrates, where their relatively long forelimbs increase the arm span and enable a firm grasp (Stalheim-Smith 1989; Thorington and Thorington 1989). In contrast, the relatively short forelimbs of *Typhlomys* (Abramov et al. 2014) restricted claw climb to primarily small and medium-sized vertical branches. The use of small vertical substrates is rather constraining, as it requires efficient grasping mechanisms of the extremities to hold firmly against gravity and enable orthograde body progression. For *Typhlomys*, vertical climb represented a very agile mode that facilitated the successful negotiation of steeply inclined substrates and permitted rapid height changes within the arboreal habitat. Reaching higher positions along substrates further assisted *Typhlomys* in gaining better perches for effective leaps.

Leap was the second most frequent locomotor mode. Leaps allow for efficient negotiation of gaps that cannot be crossed by continuous quadrupedal walk and run or by extending the body and reaching to terminal substrates. In this way, they guarantee uninterrupted locomotion beyond the reach of the tactile senses of an animal and provide access to remote arboreal locations in the canopy. Leaping percentages in *Typhlomys* were higher than those recorded for other small-sized arboreal mammals (Youlatos 1999, 2011; Urbani and Youlatos 2013; Youlatos and Panyutina 2014; Youlatos et al. 2015). The leaping activity of *Typhlomys* was probably a behavioral response to the discontinuous arboreal substrates of the experimental setup and helped the animals to efficiently overcome the challenges of arboreal gaps. These successful leaps of moderate distances (> 90% of leaps were < 40 cm) were facilitated by the long and powerful hind limbs of *Typhlomys* (Abramov et al. 2014; Panyutina et al. 2017), a morphology that favors great output during the take-off phase of leaping (Jouffroy and Lessertisseur 1979; Anemone 1993; Demes et al. 1998). To maximize efficiency during leaping, *Typhlomys* took off mainly from medium- and large-sized and obliquely- and vertically-inclined substrates. Such substrates do not deform to absorb

take off energy and align the body so that it can accelerate to a ballistically optimal trajectory (Crompton and Sellers 2007). On the other hand, most of terminal substrates were medium- and large-sized and horizontally and obliquely inclined. Such substrates provide stability and an ample platform that minimizes any risks of missing the target during landing (Demes et al. 1999).

Reversion was also another challenging locomotor mode. Rates of use by *Typhlomys* were comparable to those of *Tamiops rodolphii* (Youlatos and Panyutina 2014), but much lower than in *Sciurillus pusillus* (Youlatos 2011). Reversion is demanding as it involves an almost instantaneous 180° switch of direction, pivoting around the hind foot and including an aerial phase on the spot. This action may require ample tarsal rotations, such as hindfoot reversal, similar to that exhibited by arboreal squirrels (Jenkins and McClearn, 1984). It is unclear if *Typhlomys* is able of this kind of reversal, but it did use vertical ascent and descent and reversion in a manner similar to squirrels and other muroids.

Postural behavior was dominated by stand and cling. Both modes are dynamic and apparently suit the active profile of *Typhlomys*. This profile is reminiscent of that of other small rodents (Youlatos et al. 2015), but is different from that of small squirrels, where cling, performed exclusively by the functional claws, dominates over stand (Youlatos and Panyutina 2014). Quadrupedal stand may serve as an interim mode in between locomotor bouts and permits an active scan of suitable substrates or takeoff and landing platforms. Additionally, cling may also serve as temporary pause for adjusting on a takeoff platform or scanning for suitable landing substrates.

The overall locomotor and postural profile of *Typhlomys* indicated that the species is an adept arborealist. These results are in contrast with what is expected for a small mammal with poor eyesight. However, despite its limited visual capacity (Panyutina et al. 2017), *Typhlomys* displayed a versatile profile moving with confidence in an unfamiliar environment over inclined and vertical branches and successfully crossing gaps several times greater than the tactile reach of its vibrissae. The high rates of particularly challenging modes (i.e., vertical climb, leap and reversion) denote its competence in effective body displacement, balance maintenance, and performance of precise movements in order to successfully overcome the constraints imposed by the three-dimensional discontinuous network of unstable and variable arboreal substrates.

## Echolocation activity

During the study, *Typhlomys* were often observed to examine or detect their proximate environment and then proceed to a leap or a drop on a terminal target substrate (Panyutina et al. 2017). Recent evidence suggests that *Typhlomys* has very poor eyesight, unable to perceive the surroundings and instead uses echolocation to 'visualize' the environment (Panyutina et al. 2017; Volodin et al. 2019). Initially, we had considered that scanning behavior would be inherently related to emission of echolocation calls (Panyutina et al. 2017). However, this relation was not confirmed: the average pulse rate during scan was only 1.2 pulse/s. However, the very high variation (CV = 3.4) of pulse rate during scan indicates that sometimes echolocation calls were used for scanning the environment, whereas some other times, scanning was accomplished through olfaction or regular hearing.

Nevertheless, our study showed that body displacement in space was the sole behavior that affected the amount of emitted calls, suggesting that locomotor activity was accompanied by echolocation. This is of particular importance as it is mainly locomotion that imposes major constraints for a blind climber, and especially within an arboreal discontinuous milieu. In contrast, all non-locomotor (i.e. postural) behavior did not practically differ in their acoustic activity, which was close to zero for all categories, not only for rest. This most likely implies that a stable and secure situation does not require intense visualization of the surrounding available substrates.

Substrate type also significantly affected pulse rate, despite the fact that the mean values for the three substrate types did not differ much. Both the floor and the branches induced more pulses per second than the wire mesh wall. The floor was used considerably during both locomotor and postural behavior and was related to the exploratory activity of *Typhlomys*, inducing vocal behavior for perceiving the new environment. On the other hand, the increased pulse rate on branches was most likely related to their unstable, discontinuous nature, compelling the animals to acoustically visualize the followed paths and to trace secure initial and terminal branches during aerial trajectories. Finally, as the wire mesh was principally used for postural activities, this may explain the rather low average pulse rate on this substrate.

The idea that *Typhlomys*, when placed in the experimental enclosure, could memorize the surrounding environment and, therefore, decrease the ultrasonic pulse rate (reduce vocalization to save energy) was not been confirmed. We failed to show any monotonic dependence of the emission of echolocation calls on the time spent in the enclosure. Based on our findings, *Typhlomys* apparently employed intense emission of ultrasonic pulses during locomotion on the ground and on branches. This substantiates the importance of this sense in order to acoustically visualize the new environment and detect the available substrates within an unstable and discontinuous habitat. Moreover, as the prevailing locomotor modes were particularly challenging (e.g. vertical climb and leap) it is very likely that these calls compensate

for poor sight and enable *Typhlomys* to effectively navigate upon arboreal substrates.

## Arboreal locomotion and echolocation

The biology of *Typhlomys* is poorly known, but previous studies have reported both arboreal and burrowing habits (Abramov et al. 2014; Panyutina et al. 2017). As noted above, the animals trapped in Vietnam were collected from live traps placed on branches and from pitfall traps on the ground (Abramov et al. 2014). The present study confirms the previous observations regarding the arboreal agility and the burrowing capacity of *Typhlomys*, as the studied individuals moved easily on the branches and readily dag in the mulch of the cage, covering themselves completely (Panyutina et al. 2017). These behaviors were coupled with strictly nocturnal activity and the absence of any vocalizations in the human hearing range during the experiments (Panyutina et al. 2017; Volodin et al. 2019). In contrast, the species has developed a unique system of ultrasonic vocalizations during locomotion, which are reminiscent of bat echolocation sweeps, although their intensity is fainter (Panyutina et al. 2017; Volodin et al. 2019). This ultrasonic navigation system most likely evolved to compensate for poor vision, as the species possess very small, reduced eyes, with an inner morphology that suggests a significant visual degeneration resulting in the loss of visual acuity and focus (Panyutina et al. 2017). In general, the reduced eyes are characteristic of small subterranean or leaf litter dwellers, which mainly rely on olfaction and tactile whisking (Deschenes et al. 2012; Catania 2013) or on seismic sensitivity (Narins et al. 1997; Kimchi et al. 2005; Mason and Narins 2010) for orientation.

The degenerated eyes and the burrowing ability of *Typhlomys* are suggestive of a lineage, which probably evolved from a semi-fossorial ancestor residing in the leaf litter of tropical forests. In this scenario, visual acuity was probably lost in the leaf-litter-living stage, and when the chance to invade the arboreal habitat in the tropical forest appeared, the almost blind emigrant took advantage of this opportunity (Panyutina et al. 2017). However, the assumption that incipient echolocation evolved in the leaf litter may be reasonless, because the multiple reflections of calls in such a cluttered space would only interfere with each other. This problem is circumvented, if we consider the ancestor of *Typhlomys* as an arboreal, strictly nocturnal animal. The acquisition of incipient echolocation probably promoted safer and more efficient locomotion along and across unstable and discontinuous branches for effective escape from predators and the use of moonless dark nights for feeding. This may have provided an additional evolutionary advantage, when compared to large-eyed nocturnal mammals, which need little light. As echolocation developed as an adaptation to navigate in the darkness, vision decreased and eyes reduced in size. At some later evolutionary stage, *Typhlomys* began to explore the litter for the utilization of additional resources that could be safely collected in complete darkness, when potential predators reduce their activity. In our opinion, this scenario appears more suitable to explain the locomotion-related echolocation of *Typhlomys*.

*Typhlomys* is the only small nocturnal agile arboreal mammal that has been discovered to use ultrasonic echolocation [the relevance of ultrasonic vocalization of tarsiers to echolocation (Gursky 2019) seems doubtful], and this behavior may shed light on the evolutionary origins of echolocation in bats (Panyutina et al. 2017). Currently, there are two competing hypotheses concerning the evolution of echolocation and its presence in the paraphyletic predatory bats and absence in the monophyletic frugivorous pteropodidae bats (O'Leary et al. 2013; Tsagkogeorga et al. 2013). In the first hypothesis, the origin of echolocation followed that of flight, several times in parallel, and its absence in pteropodidae bats is plesiomorphic; in the second hypothesis, echolocation was already developed in the flying ancestral bat and was secondarily lost in pteropodidae bats (Fenton et al. 1995; Teeling et al. 2012; Thiagavel et al. 2018). The secondary loss of ultrasonic calls in the Pteropodidae, may have resulted from a shift to frugivory, increase in body size and of the larynx in particular (Panyutina et al. 2017; Thiagavel et al. 2018). The presence of ultrasonic echolocation calls and the arboreal agile habits of *Typhlomys* provide a real existing model of an echolocating, non-volant bat ancestor, as suggested by the "echolocation-first theory." This theory supports that the origin of echolocation should be traced in small quadrupedal mammals, which were adapted to fast locomotion in a complex, but poorly-lit environment (Fenton et al. 1995; Teeling et al. 2012; Carter and Adams 2015, 2016; Adams and Carter 2017; Panyutina et al. 2017). In this case, *Typhlomys* may well serve as a model for the agile quadrupedal nocturnal ancestor of bats, which had started developing ultrasonic echolocation and reducing vision (Panyutina et al. 2015, 2017). As echolocation developed progressively, vision gradually began to lose its orientation function and eye size decreased. This process in bats never reached the extremes of *Typhlomys*—interestingly, *Platacanthomys lasiurus*, the closest relative to *Typhlomys,* bears eyes that are not extremely reduced (Giarla 2017). Bat eyes are much better developed and capable of object vision, but smaller than those of visually oriented mammals (Howland et al. 2004). Considering the vision of pteropodidae bats, the group probably diverged when this sensory system was still rather well developed. This is indicated by the fact that among both fruit bats and predatory bats, there are species which have retained not only rhodopsin, but also cone opsins (Jones et al. 2013). *Typhlomys,* with its reduced eyes and poor vision and its ultrasonic echolocation, is characterized by a diverse and agile locomotor behavior, dominated by

rapid climbing on small and medium vertical branches and leaping across gaps. These behaviors may actually represent the early locomotor profile of the non-flying, but echolocating, ancestor of bats. Fast progression along and across strongly inclined arboreal substrates, supported by echolocation, could have become a pre-adaptation to leap-gliding, which helped conquer a wider array of habitats. Later adaptations to gliding and, subsequently, flapping flight were further advanced by fast navigation in the dark, enabled by the previously acquired ultrasonic echolocation.

**Author contributions** DY and MT carried out the behavioral analysis and wrote the manuscript, AAP designed the experiments, did the video recordings, performed the acoustic analysis and wrote the manuscript, IAV recorded the calls. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

# References

Abramov AV, Balakirev AE, Rozhnov VV (2014) An enigmatic pygmy dormouse: molecular and morphological evidence for the species taxonomic status of *Typhlomys chapensis* (Rodentia: Platacanthomyidae). Zool Stud 53:34

Adams RA, Carter RT (2017) Megachiropteran bats profoundly unique from microchiropterans in climbing and walking locomotion: evolutionary implications. PLoS ONE 12(9):e0185634

Anemone RL (1993) The functional anatomy of the hip and thigh in primates. In: Gebo DL (ed) Postcranial adaptation in nonhuman primates. Northern Illinois University Press, DeKalb, pp 151–174

Arkley K, Tiktak GP, Breakell V, Prescott TJ, Grant RA (2017) Whisker touch guides canopy exploration in a nocturnal, arboreal rodent, the hazel dormouse (*Muscardinus avellanarius*). J Comp Physiol A 203:133–142

ASAB/ABS (2020) Guidelines for the treatment of animals in behavioural research and teaching. Anim Behav 159:I–XI

Carter RT, Adams RA (2015) Postnatal ontogeny of the cochlea and flight ability in Jamaican fruit bats (Phyllostomidae) with implications for the evolution of echolocation. J Anat 226:301–308

Carter RT, Adams RA (2016) Integrating ontogeny of echolocation and locomotion gives unique insights into the origin of bats. J Mamm Evol 23:413–421

Cartmill M (1985) Climbing. In: Hildebrand M, Bramble KL, Wake D (eds) Functional vertebrate morphology. Harvard University Press, Cambridge, pp 73–88

Catania KC (2013) Stereo and serial sniffing guide navigation to an odour source in a mammal. Nat Commun 4:1441

Cheng F, He K, Chen ZZ, Zhang B, Wan T, Li JT, Zhang BW, Jiang XL (2017) Phylogeny and systematic revision of the genus *Typhlomys* (Rodentia, Platacanthomyidae), with description of a new species. J Mamm 98:731–743

Cong H, Liu Z, Wang Y, Wang X, Motokawa M, Hrada M, Zhou Q, Wu Y, Li Y (2013) First record of *Typhlomys cinereus* in Guangdong Province. Acta Theriol Sin 33:389–392

Crompton RH, Sellers WI (2007) A consideration of leaping locomotion as a means of predator avoidance in prosimian primates. In: Gursky S, Nekaris KA (eds) Primate anti-predator strategies. Springer, Stuttgart, pp 127–145

Demes B, Fleagle JG, Lemelin P (1998) Myological correlates to prosimian leaping. J Hum Evol 34:385–399

Demes B, Fleagle JG, Jungers WL (1999) Takeoff and landing forces of leaping strepsirhine primates. J Hum Evol 37:279–292

Deschenes M, Moore J, Kleinfeld D (2012) Sniffing and whisking in rodents. Curr Opin Neurobiol 22:243–250

Emerling CA, Springer MS (2014) Eyes underground: regression of visual protein networks in subterranean mammals. Mol Phylogen Evol 78:260–270

Fenton MB, Audet D, Obrist MK, Rydell J (1995) Signal strength, timing and self-deafening: the evolution of echolocation in bats. Paleobiology 21:229–242

Fischer MS, Schilling N, Schmidt M, Haarhaus D, Witte H (2002) Basic limb kinematics of small therian mammals. J Exp Biol 205:1315–1338

Giarla T (2017) Family Platacanthomyidae (Tree Mice). In: Wilson DE, Mittermeier RA, Lacher TE (eds) Handbook of the mammals of the world, vol 7, Rodents II. Lynx Edicions, Barcelona, pp 102–107

Grinkov VG, Palko IV, Sternberg H (2019) Character displacement within the breeding area questions reinforcement in *Ficedula* flycatchers. BioRXiv. https://doi.org/10.1101/515916

Gursky S (2019) Echolocation in a nocturnal primate? Folia Primatol 90:1–13

Hanna JB, Schmitt D, Griffin TM (2008) The energetic cost of climbing in primates. Science 320:898

Howland HC, Merola S, Basarab JR (2004) The allometry and scaling of the size of vertebrate eyes. Vis Res 44:2043–2065

Jacobs J (1974) Quantitative measurement of food selection. Oecologia 14:413–417

Jansa SA, Giarla TC, Lim BK (2009) The phylogenetic position of the rodent genus *Typhlomys* and the geographic origin of Muroidea. J Mamm 90:1083–1094

Jenkins FA Jr, McClearn D (1984) Mechanisms of hind foot reversal in climbing mammals. J Morphol 182:197–219

Jones G, Teeling EC (2006) The evolution of echolocation in bats. Trends Ecol Evol 21:149–156

Jones G, Teeling EC, Rossiter SJ (2013) From the ultrasonic to the infrared: molecular evolution and the sensory biology of bats. Front Physiol 4:117

Jouffroy FK, Lessertisseur J (1979) Relationships between limb morphology and locomotor adaptations among prosimians: an osteometric study. In: Morbeck M, Preuschoft H, Gomberg N (eds) Environment, behavior, and morphology: dynamic interactions in primates. G Fischer, Stuttgart, pp 143–181

Kimchi T, Reshef M, Terkel J (2005) Evidence for the use of reflected self-generated seismic waves for spatial orientation in a blind subterranean mammal. J Exp Biol 208:647–659

Lv X, Cong H, Kong L, Motokawa M, Harada M, Li Y (2006) The nearly complete mitochondrial genome of Chinese pygmy dormouse *Typhlomys cinereus* (Rodentia: Platacanthomyidae). Mitochon DNA Part B 1:605–606

Martin P, Bateson P (1993) Measuring behaviour: an introductory guide. Cambridge University Press, Cambridge

Mason MJ, Narins PM (2010) Seismic sensitivity and communication in subterranean mammals. In: O'Connell-Rodwell CE (ed) The use of vibrations in communication: properties, mechanisms and

function across taxa. Transworld Research Network, Trivandrum, pp 121–139

Mehta CR, Patel NR (1995) Exact logistic regression: theory and examples. Stat Med 14:2143–2160

Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference. Johns Hopkins University Press, Baltimore, pp 894–1531

Narins PM, Lewis ER, Jarvis JUM, O'Riain J (1997) The use of seismic signals by fossorial Southern African mammals: a neuroethological gold mine. Brain Res Bull 44:641–646

Niederschuh SJ, Witte H, Schmidt M (2015) The role of vibrissal sensing in forelimb position control during travelling locomotion in the rat (*Rattus norvegicus*, Rodentia). Zoology 118:51–62

Niederschuh SJ, Helbig T, Zimmermann K, Witte H, Schmidt M (2017) Kinematic response in limb and body posture to sensory feedback from carpal sinus hairs in the rat (*Rattus norvegicus*). Zoology 121:18–34

O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg SL et al (2013) The placental mammal ancestor and the Post-K-Pg radiation of placentals. Science 339(6120):662–667

Panyutina AA, Korzun LP, Kuznetsov A (2015) Flight of mammals: from terrestrial limbs to wings. Springer, Basel

Panyutina AA, Kuznetsov A, Volodin IA, Abramov A, Soldatova I (2017) A blind climber: the first evidence of ultrasonic echolocation in arboreal mammals. Integr Zool 12:172–184

Preuschoft H, Günther MM, Christian A (1998) Size dependence in prosimian locomotion and its implications for the distribution of body mass. Folia Primatol 69:60–81

Stalheim-Smith A (1989) Comparison of muscle mechanics of the forelimb of three climbers. J Morph 202:89–98

Teeling EC, Dool S, Springer MS (2012) Phylogenies, fossils and functional genes: the evolution of echolocation in bats. In: Gunnell GF, Simmons NB (eds) Evolutionary history of bats: fossils, molecules and morphology. Cambridge University Press, Cambridge, pp 1–22

Thiagavel J, Cechetto C, Santana SE, Jakobsen L, Warrant EJ, Ratcliffe JM (2018) Auditory opportunity and visual constraint enabled the evolution of echolocation in bats. Nat Commun 9:98

Thorington RW Jr, Thorington EM (1989) Postcranial proportions of Microsciurus and Sciurillus, the American pygmy tree squirrels. In: Redford KH, Eisenberg JF (eds) Advances in neotropical mammalogy. Sandhill Crane Press, Gainesville, pp 125–136

Tsagkogeorga G, Parker J, Stupka E, Cotton J, Rossiter S (2013) Phylogenomic analyses elucidate the evolutionary relationships of bats. Curr Biol 23(22):2262–2267

Urbani B, Youlatos D (2013) Positional behavior and substrate use of *Micromys minutus* (Rodentia: Muridae): Insights for understanding primate origins. J Hum Evol 64:130–136

Volodin IA, Panyutina AA, Abramov AV, Ilchenko OG, Volodina EV (2019) Ultrasonic bouts of a blind climbing rodent (*Typhlomys chapensis*): acoustic analysis. Bioacoustics 28(6):575–591

Wang Y, Li C, Chen Z (1996) Taxonomy, distribution and differentiation of *Typhlomys cinereus* (Platacanthomyidae, Mammalia). Acta Theriol Sin 16:54–66

Wu D, Wang G (1984) A new subspecies of *Typhlomys cinereus* Milne-Edwards from Yunnan, China. Acta Theriol Sin 4:213–215

Wilson DE, Reeder DM (2005) Mammal species of the world: a taxonomic and geographic reference, vol 2, 3rd edn. Johns Hopkins University Press, Baltimore

Youlatos D (1999) Locomotor and postural behavior of *Sciurus igniventris* and *Microsciurus flaviventer* (Rodentia: Sciuridae) in eastern Ecuador. Mammalia 63:405–416

Youlatos D (2011) Substrate use and locomotor modes of the neotropical pygmy squirrel *Sciurillus pusillus* (E. Geoffroy, 1803) in French Guyana. Zool Stud 50:745–750

Youlatos D, Panyutina A (2014) Habitual bark gleaning by Cambodian striped squirrels *Tamiops rodolphii* (Rodentia: Sciuridae) in Cat Tien National Park, South Vietnam. Mamm Stud 39:73–81

Youlatos D, Karantanis NE, Byron C, Panyutina AA (2015) Pedal grasping in an arboreal rodent relates to above-branch behavior on slender substrates. J Zool 296:239–248

**CORRECTION**

# Correction to: Locomotion and postures of the Vietnamese pygmy dormouse *Typhlomys chapensis* (Platacanthomyidae, Rodentia): climbing and leaping in the blind

Dionisios Youlatos[1] · Aleksandra A. Panyutina[2] · Makrina Tsinoglou[1] · Ilya A. Volodin[3]

**Correction to: Mammalian Biology**
https://doi.org/10.1007/s42991-020-00043-9

The original version of this article unfortunately contained a mistake. The caption of Fig. 4 was incorrect. The corrected Fig. 4 caption is given below.
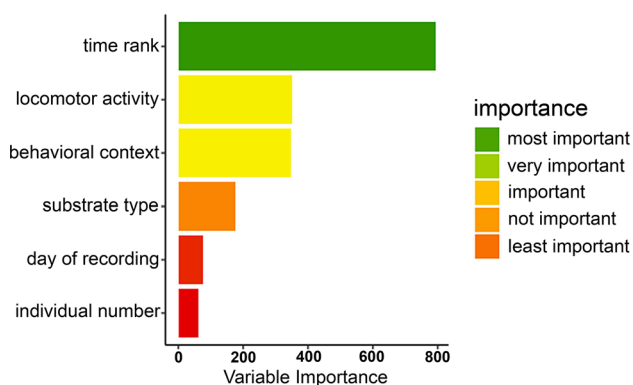


**Fig. 4** Importance of different factors for predicting the emission of echolocation calls (pulse rate), using the random forest algorithm (yellow indicates an intermediate gradation between important and very important)

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

The original article can be found online at https://doi.org/10.1007/s42991-020-00043-9.

✉ Dionisios Youlatos
  dyoul@bio.auth.gr

1 Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece

2 Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

3 Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia

Springer