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Reproduction, postnatal development and resting metabolic rate of a poorly studied subterranean rodent, the long-clawed vole (*Prometheomys schaposchnikowi*)

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Abstract

The long-clawed vole (LCV) is a poorly studied species endemic to the Caucasus Mountains. It is a rare example of a small subterranean rodent living in a cold climate. Subterranean lifestyle and low ambient temperatures are thought to affect an animal's "pace-of-life" in opposite directions, and it is currently unknown how LCV solve this trade-off. We report key aspects of reproduction and postnatal development as well as resting metabolic rate (RMR) and low critical temperature (T_{lc}) in captive LCV. Mean litter size was 2.9 (± 0.9 SD, range 1–4) and gestation lasted 32–33 days. The embryonic and pre-weaning postnatal growth rate was low when adult weight of 80–90 g was taken into account (0.14 g/day and 0.8 g/day, respectively). Juveniles developed very slowly (eyes opening at 22–25 days) and weaned at about 1 month. Members of breeding pairs exhibited permanent nest cohabitation. Males were present at birth and displayed paternal care of pups. Females may become pregnant by 50 days or even earlier. The T_{lc} was estimated as 18.9 (± 0.9 SE) °C. The mass-independent basal metabolic rate (BMR) was 1.65 (± 0.08 SD) mL O₂/g × h, which is close to the expected value calculated from the allometric relationship between body mass and BMR determined for other voles adapted to similar climate conditions. The unusual combination of several slow life history traits with relatively early sexual maturation and unreduced BMR apparently constitute elements of the unique adaptive complex of the relatively small, strictly herbivore subterranean rodent living in cold humid habitats.

Keywords *Prometheomys schaposchnikowi* · Arvicolinae · Subterranean rodents · Life history · Reproduction · Basal metabolic rate · Low critical temperature

Introduction

Evolutionary ecologists have long used subterranean rodents for studying adaptive convergence and divergence at different levels of organization (Nevo 1979; Lacey et al. 2000; Begall et al. 2007). This ecological specialization is associated with severe selection pressures on morphology, physiology, behavior and life-history traits. In comparison with

surface-dwelling rodents, subterranean species are thought to display slow "pace of life"; in particular, low mass-independent metabolic rate, slow growth and development, late sexual maturation, small litter size and long lifespan (McNab 1966; Nevo 1979, 1999; Bennett et al. 2000; Buffenstein 2000; Busch et al. 2000; Begall et al. 2007). However, the ultimate factors underlying some of these characteristics and their variability among the subterranean species are not well understood (Busch et al. 2000; White 2003; Bozinovic et al. 2005; Luna et al. 2009, 2017). New information on poorly studied subterranean taxa can thus bring new insight to these issues.

The long-clawed vole (LCV, *Prometheomys schaposchnikowi*) represents one of the most basal lineages in the subfamily Arvicolinae (Abramson et al. 2009, 2021; Steppan and Schenk 2017; İbiş et al. 2020), and is one of only two "truly subterranean" arvicoline genera (the other one is *Ellobius*, mole voles—Gromov and Polyakov 1977; Lacey et al. 2000). The LCV exhibits several pronounced

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morphological modifications associated with living underground, the most obvious of which contained in its common name: the long, strong claws of the forelimbs. Its lumpy body, blunt muzzle and tiny eyes (Fig. 1), feeding behavior, and the architecture of the extended burrow systems all support its subterranean specialization (Turov 1926; Spitzenberger and Steiner 1964; Gambaryan et al. 1957; Gambaryan 2002; Vereshchagin 1959; Vorontsov 1966; Zimina and Yasny 1977). In addition, a recent molecular study has revealed the signatures of selection in several mitochondrial protein-coding genes known to be associated with subterranean lifestyle (Bondareva et al. 2021).

The LCV now occupies only a small range in the Caucasian Mountains and north-eastern Turkey (Kryštufek and Vohralík 2005). Preferred habitats are mesic tall-grass sub-alpine meadows and pastures at elevations of 1.500–2.500 m a.s.l. (Vereshchagin 1959; Vorontsov 1966; Kryštufek and Vohralík 2005). A cold, alpine climate with high humidity prevails at these elevations. The mean annual temperature is 0.5 °C, the average monthly maximum (July) and minimum (January) temperature are 16.5 °C and – 14 °C, respectively. The occurrence in habitats with a cool climate and moist soils is rather unusual for subterranean rodents, most of which are distributed in warmer and more arid areas (Lacey et al. 2000; but see S1 in Luna et al. 2017 for the range of climatic conditions).

Currently, very little is known about the reproductive biology of LCV. These voles live in monogamous pairs. Reproduction lasts from late May to August with two successive litters in a season. The average number of embryos is 3.1–3.8 (Yatsenko 1959; Spitzenberger and Steiner 1964; Zimina and Yasny 1977). Yatsenko (1959) provided fragmentary data on ontogeny, but noted that all attempts to breed this species in captivity had failed. Even basic characteristics of life-history such as pregnancy duration, offspring



Fig. 1 Adult long-clawed vole. Notice small eyes and long, strong claws of the forelimbs

growth and development rate and age at sexual maturity are currently unknown, and any physiological parameters are also unavailable. Nonetheless, the unusual combination of traits in this species, namely, a subterranean lifestyle in a cold humid climate, could make such data a valuable addition to our understanding of the underground “pace of life”. Do LCV have a low basal metabolic rate (BMR) expected for a subterranean rodent, or, on the contrary, an increased BMR as a species that evolved in a low-temperature environment (McNab 1992; Lovegrove 2003; Fristoe et al. 2015; Luna et al. 2017)? If the latter is true, do its reproductive characteristics reflect the selection for a slow life history, which can be predicted based on the subterranean specialization, or do they support the evolutionary association between life history and the metabolic rate postulated by the “pace-of-life syndrome” hypothesis (Ricklefs and Wikelski 2002; Glazier 2015; Dammhahn et al. 2018) and the Metabolic Theory of Ecology (Brown et al. 2004)? The aim of this study was to obtain the reproductive and metabolic data necessary to answer these questions.

Materials and methods

Animals and housing conditions

Six females and seven males (apparently, all were the young of the year) were trapped in the Main Caucasus Range (N42.63° W44.13°, elevation 2140–2200 m a.s.l.) and brought to St. Petersburg State University in July 2019. The animals were housed in glass terraria (100×70×40 cm and 120×70×40 cm) each containing about 20 cm of substrate and equipped with two wooden boxes (25×15×20 cm) and two glass tunnels (45×5×5 cm and 60×8×8 cm). During the first year of the study, commercial rodent bedding (FIX) was used as substrate, but then a mix of wood shaving and dried sphagnum turned out to be preferable. Tissue paper was used as nesting material. Voles were fed ad lib with carrots, fresh lettuce, apples, commercial rabbit pellets, and cereals. The diet was supplemented weekly by liquid vitamin D3 (dripped on a slice of bread), and willow, pine and larch twigs. No water was offered. Toilet areas were cleaned and spoiled leftovers were removed each other day, whereas full cleaning was carried out once a month. The breeding colony was maintained under a 16 h light: 8 h dark photoperiod. In addition to visible lighting, one Exo Terra Repti Glo 10.0 Compact Tropical Terrarium Lamp was established over each terrarium. Ambient temperature ranged from 16 °C in winter to 23 °C in summer.

Voles were kept as monogamous pairs during the whole observation period. At first, new heterosexual pairs were established so that pair-mates originated from different burrows. After deaths of some individuals, their partners were

mated with unrelated voles of the first laboratory generation. In most cases, the voles were not disturbed after pairing, with the exception of cleaning the toilet areas and weighing the animals, which was performed once every 2–3 weeks.

Collecting and analyzing reproductive data

Five adult females of the first laboratory generation were examined daily for vaginal condition during the first week after pairing, and vaginal smears were taken if possible. The smears were air-dried, stained with the May-Grünwald solution and analyzed later with a light microscope at magnification 280X. Two intervals from occurrence of spermatozoa or vaginal plug to parturition, one interval from observed coitus to parturition, four shortest intervals from the pairing to the birth of the first litter, and six shortest inter-birth intervals were used to estimate pregnancy duration.

To control the physical and reproductive condition of the animals, short but regular (20–90 min each other day or, in cases of pregnant females, daily) behavioral observations were carried out. We were usually able to observe the voles' behavior outside the nest and sometimes in the nest (through the glass bottom of the terrarium).

Three wild-caught females, three wild-caught males, and four pairs of the first laboratory generation took part in the breeding. In total, they produced 28 litters. Most of the offspring died in the first days after birth, and additional high mortality was observed later. In some cases, the possible cause was anxiety of adult animals on the first days after or shortly before birth; the rest died of unknown causes. Due to the high pup mortality along with our efforts to reduce it by minimizing the parental disturbance as much as possible, sample sizes used for the estimates of different life history parameters varied (Table 1). In most cases, we did not take newborns on the day of birth for inspection and measurements. Newborns often could be seen and counted through the bottom of the terrarium. Offspring were weighed and inspected for the developmental traits (fur condition, incisors eruption, pinna formation, separating of digits, opening of eyes) at least every 2nd–5th day from 0–3 to 30 days of age and approximately once a week afterward until growth stopped. Inspections

were skipped if the parents showed signs of severe anxiety, such as retrieving pups from one to another nest box. Locomotory patterns, self-grooming, scratching, vocalizations, feeding solid food, defensive behavior at handling as well as all interactions among littermates and between the young and their parents were recorded on an ad hoc basis. Growth parameters were calculated using the Gompertz equation (Zullinger et al. 1984) for individuals for which a complete data set from days 0–3 to days 90–99 was available: $m(t) = A e^{-e^{-K(t-I)}}$, where $m(t)$ = body mass (g) at time t (days), A = asymptotic value (g), e is Euler's number, K = growth constant (days^{-1}), and I = age at the inflection point (days). All three growth parameters were estimated using the Levenberg–Marquardt algorithm. Individual growth curves (Fig. 2) were fitted with local polynomial regression using the 'loess' function in R (R Core Team 2022).

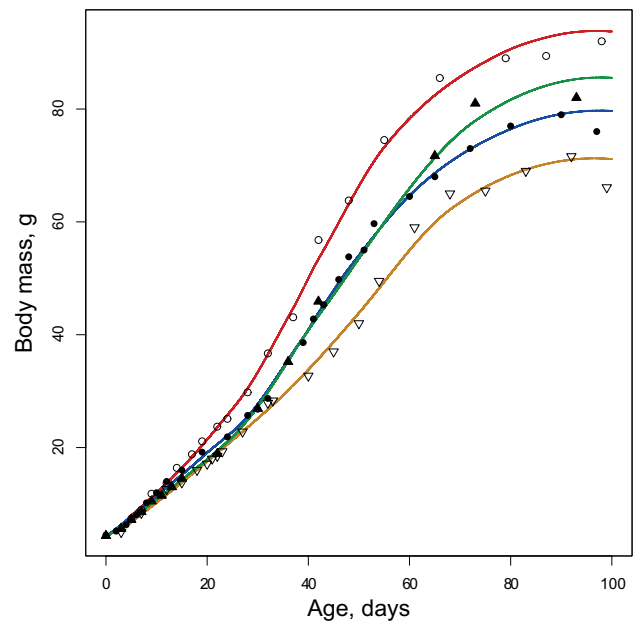


Fig. 2 Growth curves for juvenile long-clawed voles from four litters. Each point indicates average weight for two littermates. Different litters are denoted by different markers

Table 1 Sample sizes used for the estimates of life history parameters of the LCV

Parameter	Number of litters = sample size	Number of offspring	Number of parenting pairs
Litter size at birth	22	60	7
Neonate linear measurements	3	6	2
Neonate weight	6	10	3
Weight growth rate and development from days 0–3 to day 30	5	10	3
Growth parameters from days 0–3 to days 90–99	4	8	3

Collecting and analyzing metabolic data

The subjects used for the estimation of thermo-neutral zone (TNZ) and resting metabolic rate (RMR) measurements were six adult females (minimum age 134 days) and three adult males (minimum age 440 days). All of them except one male were laboratory-born offspring of two different pairs. None of the females were pregnant as confirmed by the behavioral and weight monitoring over the next 4 weeks. These animals were kept under the same condition described above. The metabolic experiments took place between February 9th and 16th, 2021. During this period and for the previous 2 months, the ambient temperature in the colony room was 16–17 °C which appears to be close to the average summer temperatures near the soil surface reported for similar elevation of Georgia (Elizbarashvili et al. 2010).

We assessed the RMR of nine LCV (two males and seven females) by flow-through respirometry. After a preliminary food deprivation for 2.5 h, we placed four voles in 2.6 L cylindrical polypropylene chambers. The chambers were placed in a Panasonic MIR-154 incubator, which maintained the temperature with an accuracy of 0.5 °C. The temperature in the chambers (T_a) was recorded using iButton® thermologgers with an accuracy of 0.5 or 0.125 °C. Given the polyphasic daily activity pattern of *Prometheomys* (Gambaryan et al. 1957; Smorkatcheva and Nikitina, unpublished), the metabolic experiments took place in two daily sessions. The first session started at 11–12 am and the second one at 6–7 pm. One of the males began to show signs of stress after three metabolic trials and was replaced by another one.

Using five membrane pumps, outside air was pumped through chambers with indicator silica gel. Then, the dried air was pushed through the chambers with animals at a rate of about 870 mL/min. To measure RMR of several animals in one session, we used a flow switching system, which in automatic mode alternately sent air from chambers with voles and from an empty (reference) chamber to the Fox-Box respirometer (Sable Systems, USA). In one session, we measured RMR in four voles. Each vole was measured for 20 min (10 min for the reference chamber), and then the channel was switched to the next chamber. Each metabolic trial included four complete cycles that lasted about 7 h in total.

The air leaving the metabolic chamber passed through a 70 mL chamber with a Drierite® desiccant and then through the FoxBox mass flow-meter. Air at a flow rate of 100 mL/min was then subsampled to the FoxBox O₂ and CO₂ gas analyzers. The fractional concentrations of O₂ and CO₂ in the air entering and leaving the chamber with the animal were recorded with a sampling interval of 3 s. We discarded the first 5 min of measurements, because after switching the channel, the system needed 2–3 min for the gas concentrations to come to a new stable value (wash-out time). To

estimate the RMR, we used the running minimum 5-min average. Before each measurement session, the gas analyzers were calibrated using 6.0 nitrogen and span gas (mixture of 21.5% O₂ and 0.495% CO₂ in N₂). Other respirometry details are provided elsewhere (Bushuev et al. 2018, 2021).

The volume of oxygen consumed by the animals per unit of time was calculated from the flow rate of air leaving the metabolic chamber and the relative concentrations of O₂ and CO₂ in the incoming and outgoing air using Haldane transformation (see the equation in Bushuev et al. 2018). The animals were weighed both before and after the metabolic trials. To calculate the mass-specific RMR, we used the body weight of the animals after the trial, since it was more strongly related to the RMR within TNZ ($R^2 = 0.959$ and $R^2 = 0.970$ for body weight before and after the trial, correspondingly). We excluded data from individuals that did not become quiescent and did not show low steady-state oxygen consumption during the trial. We carried out RMR measurements for all individuals at the following temperature settings of the incubator: 10.0, 15.0, 17.5, 20.0, 22.5, and 23.5 °C. Since the estimation of the upper critical temperature (T_{uc}) was not part of our tasks, we did not use higher T_a settings once we were sure we had reached the lower TNZ limit. We did not attempt to estimate T_{uc} due to the risk of overheating the animals at T_a above the TNZ.

To estimate the lower critical temperature (T_{lc}) and the slope of the RMR dependence on the T_a , we used a segmented (piecewise) linear regression (Muggeo 2003, 2016, 2017). The parameters of the segmented regressions were calculated using the ‘segmented’ function from the R (R Core Team 2022) package ‘segmented’ (Muggeo 2008). This analysis was done without the data from two females who showed pronounced signs of obesity, which according to Genoud et al. (2018) is important evidence of abnormal physical condition in the studies on metabolic rate of mammals.

A rectal body temperature (T_b) was measured using an OM-EL-GFX-DTC temperature logger (Omega, USA) and K-type thermocouple (\varnothing 1.5 mm). To ensure the T_b measurement accuracy of 0.1 C, the thermologger was calibrated with a mercury thermometer.

Means are given with \pm SD unless otherwise stated.

Results

Duration of pregnancy and birth intervals

On the day of pairing, leukocytes predominated in vaginal smears in all five females examined. After housing with males, all females showed changes typical of the estrous cycle. On day 4, the vaginal smears of two females contained scales and spermatozooids, and three females had vaginal

plugs. Two of these females gave birth 32 days after mating (36 days after pairing). Other recorded intervals from pairing to the birth of the first litter were 34, 35, 35, 38, 116 and 125 days. The interval between the observed coitus and parturition was 33 days. Six of 17 inter-birth intervals (35%) fell between 33 and 36 days which apparently corresponded to successful conceptions during postpartum estrus. The duration of the rest ranged from 51 to 273 days. It should be recognized, however, that with our method of data collection some deliveries could be missed. Maximum reproductive outputs registered for a pair of wild-born voles was 11 litters over a 30-month period with last three litters separated by intervals of about nine months.

Litter size

Seven females gave birth to 28 litters. Thirteen of these were obtained from the wild-born pairs, and 15 were born to the voles of the first laboratory generation. Twenty one litters ranged between 1 and 4 pups with a mean 2.86 ± 0.85 and a mode of 3. In the remaining seven cases, squeaks from the nest indicated birth, but birth litter sizes were not determined.

Development (Fig. 5, Online Resource 1)

As most muroid rodents and all arvicoline species, LCV are altricial at birth. Neonates were pink, wrinkled and hairless. The eyes were closed, the pinnae were not detached, the incisors were not erupted, and digits were fused. White claws were clearly visible on both hind and fore digits. By day 2, the dorsum was pigmented. Very short sparse hairs on the back and body sides and longer vibrissae on cheeks were visible. By days 3–5, pinna was unfolded. By day 6, the back was covered with very short (velvet) gray fur; sparse light hairs were barely noticeable on the venter and limbs. The fore digits began to separate, and their claws began to bend. By day 10, the whole body was covered with short fur which was lighter and sparser on the belly and inner sides of the legs. A black stripe was sometimes barely visible along the ridge; it completely disappeared after a few days. The separation of the fore digits was completed. The sole pads were well-developed. Pups actively crawled and huddled when in the nest but remained motionless when removed. By day 14 both low and upper incisors were erupted, and the hind toes were completely separated. In females, two pairs of inguinal nipples were visible through the light thin fur on the belly. At this age, the pups from one of the litters began to emit, in addition to the loud squeak typical for all rodent pups, a quiet cat-like purring which is produced almost constantly by adult LCV. In other young, this vocalization was noted at about 3–4 weeks of age. By day 20 juveniles walked, ran quickly and stood with support on the walls of the cage. The

comfort behavior (washing of the face and other parts of the body, scratching) was also developed. By days 22–25 the eyes opened. At 25 days, the young started to explore the area around the nest, dig awkwardly, and feed in the tunnels. By 30 days of age, the young ran forwards and backwards through the tunnels, like adult animals. During the following 10 days, they became fully involved in the transport of food and nest material from outside the tunnels into the tunnels and the nest. Defensive behavior (attempts to bite at handling) was registered for the first time in 30-day old voles. Based on the captive observations, we aged the smallest wild voles caught at the burrow entrances to be 25–30 days, judging by their body weight and general appearance. The smallest young were trapped together with their mother and still nursed, as did 1-month-old juveniles in captivity.

Littermates at the age of 30–45 days often displayed affiliative behavior like huddling and allogrooming. When two juvenile littermates met in the tunnel, one of them sometimes jumped and pounced on the other, a behavior we considered as social play. At the age of 75–85 days, both male and female offspring living with parents started to display the stereotypic behavior—route-tracing and jumping. At this stage, aggressive interactions between the grown offspring and their parents were occasionally observed.

In four females kept with their parents, the vagina opened at 60, 66, 66 and 68 days. A wild-born female which was, as judging by its weight and general appearance, not older than a month of age at capture, was mated 12 days later with an adult male. She gave birth 38 days after pairing which indicated the successful mating at the age of approximately 45–50 days. None of three captive-born females kept with their parents for 5–7 months were observed to mate or exhibit signs of pregnancy. The minimum age of male fertility remains unknown.

Growth

Neonates had an average body weight of 4.43 ± 0.07 g (5.7% of adult body mass; $N=3$ litters, each including one male and one female juveniles). Head and body length was 48 ± 1 mm; tail length was 7.5 ± 1 mm.

Average growth rate of the young during the first 30 days after birth was 0.80 ± 0.10 g/day. The complete (until adulthood) growth curve showed a clear sigmoidal shape (Fig. 2). Growth parameters calculated according to the Gompertz equation in individuals that had reached adult weight and stopped growing were: A (asymptotic value) = 95.0 ± 15.2 ; $K = 0.034 \pm 0.003$ days⁻¹, and $I = 34.6 \pm 3.9$ days.

Parental behavior

All pairs exhibited permanent nest cohabitation, and fathers were observed to be present at birth. Both parents

displayed increased digging, nest-building, and feeding activity the day before birth, but remained almost permanently in the nest in the first day postpartum. While nursing, the mother either laid over the pups or took a position on her side or on her back. An arched-back position, typical for nursing females of many small rodents, was never observed. Juveniles never attached to the mother's nipples, dragging behind her as she moved through the tunnels. Sires huddled and groomed the pups when in the nest and dragged back those that happened to be outside the nest. Unlike the parents of some other arvicoline, adult LCV never tried to transport older juveniles that walked out of the nest. In general, there was an impression of a rather careless attitude of the parents toward the offspring around weaning.

Longevity

Seven of 13 individuals brought to St. Petersburg in summer 2019 died during the first year in captivity, three voles lived for 20–27 months, and 3 are still alive. The minimum age of these animals can be estimated as 37 months, and the reproductive lifespan in two of them extended until at least 33 months.

Metabolic rate

The relation between mass-specific RMR and ambient temperature (T_a) is shown on Fig. 3. The low critical temperature (T_{lc}) was estimated as 18.9 °C (SE = 0.9). The regression of mass-specific RMR on T_a in the range below T_{lc} was described by the equation $RMR = 4.667(\pm 0.230) - 0.158(\pm 0.015) \times T_a$. The slope of this regression cannot be used as the mean minimal thermal conductance of LCV since their thermoregulation strongly deviated from the Scholander-Irving model: the regression line intersected the X-axis at the $T_a = 29.6$ °C (SE = 2.86), while the model suggests that it extrapolates to the body temperature (T_b). Interestingly, usually the use of this slope overestimates T_b (McNab 1980), while in the case of LCV, there was a clear underestimation, since T_b in LCV was 37.2 ± 0.83 °C ($N = 7$). This T_b value is consistent with published data on other arvicoline (McNab 1992).

RMR within the zone of thermoneutrality, estimated from 11 measurements in six individuals, was 1.65 ± 0.08 mL O₂/g × h (body weight = 76.55 ± 14.49 g) and can be used as an estimate of BMR of the long-claw vole. The mass-specific BMR of two fat individuals was 1.17 ± 0.05 mL O₂/g × h with a body weight of 128.66 ± 6.62 g (averaged over 5 measurements on different days).

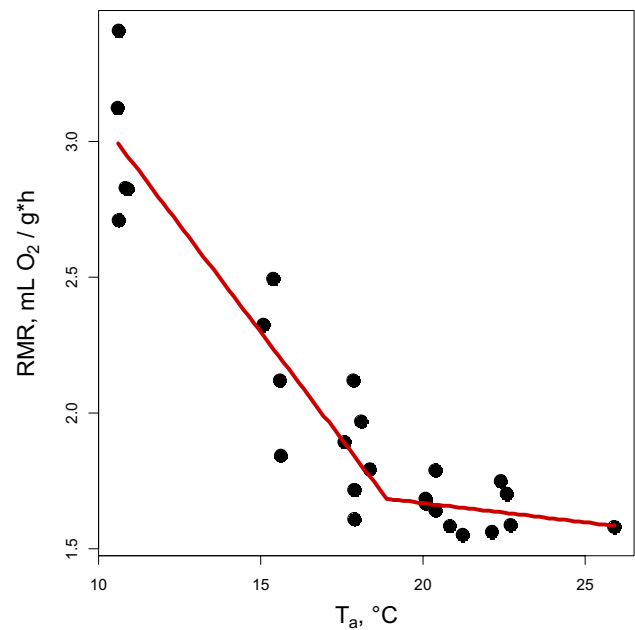


Fig. 3 Relationship between resting metabolic rate (RMR) and ambient temperature (T_a) in the long-clawed vole

Discussion

In this study, several basic life-history parameters of the LCV have been determined for the first time. The pregnancy duration in this species is 32–33 days. This is longer than the gestation of any other vole, including the subterranean *Ellobius* as well as two much larger semi-aquatic arvicoline—the muskrat, *Ondatra zibethicus*, and the round-tailed muskrat, *Neofiber alleni*. (Fig. 4; see Table S1, Online Resource 2, for database and references). Smorkatcheva et al. (2016) provided the allometric relationships between body mass and several reproductive variables in surface-dwelling voles. We used these regression equations to calculate embryonic and postnatal growth rates, birth mass and weaning mass predicted for LCV, given female weight of 90 g. These values were compared with the respective empirical values obtained in our study (Table 2). Embryonic growth rate in LCV turned to be extremely low, falling out of the 95% prediction limits. On the other hand, the birth weight is quite close to the expected value (Table 2) due to a combination of protracted pregnancy and low growth rate. Therefore, this subterranean vole exhibits neither the tendency toward precocity, as characteristic of *Ellobius* (Smorkatcheva et al. 2016), nor the trend to altriciality, as described for subterranean species of the suborder Hystricomorpha (Bennett et al. 1991; Begall et al. 1999; Camin 2010). Offspring growth rate between parturition and weaning is slightly lower, while weanling body mass is higher than

Fig. 4 Pregnancy duration (dark bars) and, if available, the intervals from conception to opening of eyes (light bars) in 19 genera of voles. For the genera displaying inter-species variation, the limits are denoted by whiskers. See Table S1, Online Resource 2 for data set and references

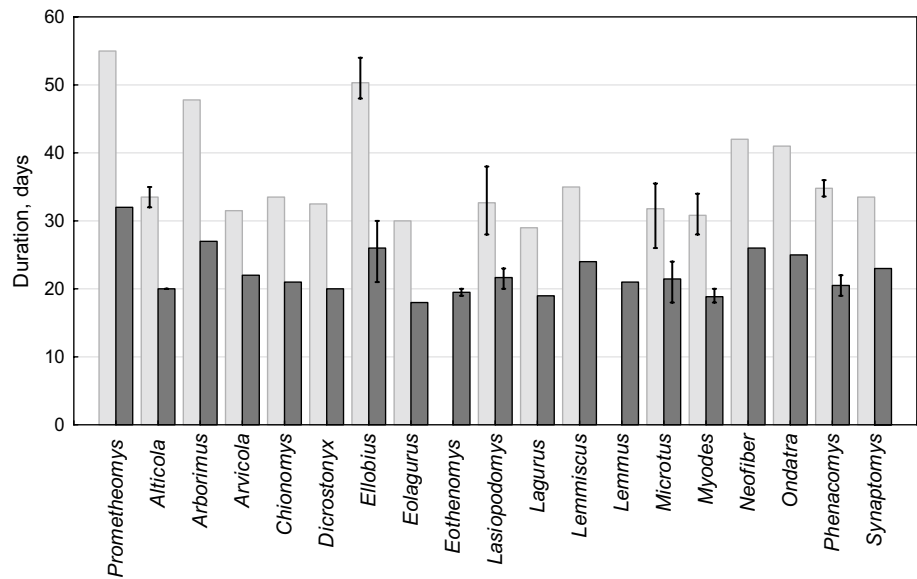


Table 2 The comparison between empirically determined and theoretically predicted values of the long-clawed vole's life-history parameters

Reproductive characteristic	Regression for non-subterranean voles	Predicted value	Revealed value	Deviation from the predicted value (%)
Embryonic growth rate, g/day	$-0.23 + 0.23 \times \log_{10}(\text{Body Mass})$	0.219	0.138	-37*
Postembryonic growth rate, g/day	$-0.67 + 0.83 \times \log_{10}(\text{Body Mass})$	0.952	0.802	-16
Relative neonatal body mass, %	$15.15 - 5.11 \times \log_{10}(\text{Body Mass})$	5.16	4.90	-5.0
Relative weaning (at 30 days) body mass, %	$86.82 - 33.47 \times \log_{10}(\text{Body Mass})$	23.2	31.4	+35

The predicted values were calculated using the regression equations obtained for non-subterranean voles (Smorkatcheva et al. 2016) and average female body mass of 90 g

The asterisk denotes the value that is out of the prediction interval (Smorkatcheva et al. 2016)

it is predicted for a surface-dwelling vole, given the adult body mass. Both parameters are, however, within the 95% prediction limits (Table 2). A comparison of LCV's postnatal development with that of other arvicolines indicates sequence heterochrony within the subfamily: while opening of eyes and eruption of incisors are exceptionally delayed, the timing of pinna unfolding and toe separation is well within the range of other voles (Table S1, Online Resource 2). The interval from conception to eyes opening may be used as an integral indicator of developmental rate (Burda 1989). This interval is longer in LCV than in any other arvicoline (Fig. 4). On the other hand, female LCVs seem to attain fertility relatively early. Our record of a successful pregnancy in a female at about 50 days or younger supports the published observations of pregnant young of the year with a body weight half that of adults (Yatsenko 1959). Given the very limited amount of data available, the minimum age of female fertility may be even younger. This contrasts with the delayed embryonic and pre-weaning growth and development of this species. This also contrasts with the dramatically delayed first breeding

in female *Ellobius* (2.5—12 months—Evdokimov 2001; Smorkatcheva et al. 2016; Kaya and Coşkun 2015).

The average and modal numbers of newborns (2.9 and 3, respectively) were very similar or somewhat lower than the respective values based on the embryos counts and implantation sites in the field (3.1 and 3—Zimina and Yasny 1977; or 3.5 and 4—Yatsenko 1959). Similar differences between litter sizes obtained for the same species by two methods are not unusual in voles (Bashenina 1975; Nadeau 1985; Fernández-Salvador et al. 2001; Smorkatcheva et al. 2016) and may reflect either early neonate mortality or lower fertility under captive conditions. Regardless, both field and captive values suggest relatively low breeding intensity, especially when long inter-birth intervals are taken into account.

Permanent sharing of the litter nest by the male and female as well as male parental behavior confirm the previously reported monogamy of this species (Turov 1926; Yatsenko 1959). It is important to emphasize that the wild-trapped males were observed to display paternal care from the first days after the birth of their first laboratory-born litters. Therefore, their parental responsiveness is unlikely an

artifact of laboratory conditions (for example, the result of sensitization due to the forced cohabitation with a dam and pups—e.g., Rosenblatt 1967; Horrell et al. 2017).

To summarize this section, like most other subterranean species including the members of a closely related genus *Ellobius* (Letitskaya 1984; Kaya and Coşkun 2015; Smorkatcheva et al. 2016), LCV display low growth and development rate, high investment per offspring and low overall reproductive investment. Given a very high mortality of juveniles, one could have supposed that our estimates of reproductive parameters are underestimated and are an artifact of housing conditions inappropriate for this species. We rule out this possibility based on a good correspondence between the weight of captive juveniles that had recently opened their eyes and the minimum weight of young voles trapped in nature (24–27 g—Yatsenko 1959). The reproductive characteristics common for LCV and other subterranean rodents are usually considered to evolve due to living in the relatively safe and stable environment (Nevo 1979, 1999; Busch et al. 2000; Buffenstein 2000; Sibly and Brown 2007). However, the absence of the significant delay of first breeding, one of the key attributes of slow life history (Gaillard et al. 2005; Dobson and Oli 2007), is not consistent with low extrinsic mortality as a main selective force for the phenomenal extended embryonic and early postnatal development in LCV. Although LCV are unlikely to be subject to strong predation pressure, they may be vulnerable to adverse climatic conditions of highlands even in their burrows. Specifically, they have been reported to suffer from high mortality in the spring, when tunnels are flooded with water which subsequently freezes (Bukhnikashvili and Kandaurov 1998). We suggest that the trade-off between allocation energy to reproduction and digging is a primary or additional ultimate cause of low reproductive investment in LCV, as has been proposed by some authors for mole voles (Moshkin et al. 2007). These voles are strictly herbivorous, at least during the growing season (Gambaryan et al. 1957; Vorontsov 1966; Zimina and Yasny 1977). Above-ground parts of plants represent less valuable resource in terms of nutritional value than subterranean plant tissues (Buffenstein 2000). Food specialization coupled with energetic costs of foraging by digging (Vleck 1979), relatively small body size, and significant thermoregulatory expenditure associated with living in highlands may limit the amount of energy that can be allocated to reproduction.

Among animals of similar body mass, cold-adapted species have a higher BMR, lower T_{lc} , and a gentler slope of the regression of RMR on T_a (Fristoe et al. 2015). The low T_{lc} in LCV (18.9 °C) is close to that in such Arctic species of similar size as *Dicrostonyx groenlandicus* (T_{lc} = 19.2 °C according to Klaassen et al. 2002; T_{lc} = ~ 16 °C according to Fig. 6b in McNab 1992), *Lemmus sibiricus* (T_{lc} = 10–19 °C, depending on season and year; Coady 1975) and *L. trimucronatus*

(T_{lc} = 16.9 °C; Klaassen et al. 2002). On the other hand, the slope of the regression of RMR on T_a (equal to the mean minimal thermal conductance in mL O₂/g × h × °C if the regression extrapolates to T_b when the rate of metabolism is zero) in LCV was equal to 0.158, which is too steep for cold-adapted species. This slope in species similar in body weight to the LCV usually is in the range of 0.07–0.13 (e.g., Drożdż et al. 1971; Coady 1975; McNab 1992). Although the low T_{lc} in the LCV reflects its adaptation to cold conditions at high altitudes, the steep RMR slope shows that this species is not thermoregulatory adapted to significant changes in T_a . This could be associated with the relative constancy of T_a in LCV burrows.

Truly subterranean rodents have long been thought to have reduced mass-independent BMR compared with that of surface-dwelling species of the same body size (McNab 1966; Nevo 1979, 1999; Bozinovic et al. 2005; Luna et al. 2009, 2017; Šumbera 2019). On the other hand, the comparative phylogenetic analysis conducted by White (2003) has not shown any difference in BMR between strictly subterranean and semifossorial mammals being heavier than 77 g or inhabiting mesic rather than arid environment. In addition, a negative correlation between ambient temperature and BMR has been shown for mammals in general (Lovegrove 2003) as well as for terrestrial rodents (Naya et al. 2013), subterranean rodents (Luna et al. 2017), and arvicolines (McNab 1992). Keeping these facts in mind, there is no clear prediction for a subterranean vole with a body mass of 70–90 g (mean 74 g—Yatsenko 1959) living in a cold damp climate of highlands. It was unclear whether the LCV's mass-specific metabolic rate would be lower than would be expected for a surface-dwelling vole living in low-temperature environment. To address this question, we collected and analyzed the available high-quality BMR data (Genoud et al. 2018) for the surface-dwelling voles whose sites of origin are characterized by annual mean T_a close to this of the subalpine zone of the Greater Caucasus (N = 11, see Online Resource 3 for the strategies of T_a data obtaining, metabolic data selection, and statistical analysis; see Online Resource 2, Table S2 for the dataset). The obtained allometric relationship between body mass and BMR was $10.663(\pm 5.033) \times M^{0.565(\pm 0.137)}$. The predicted BMR value for LCV calculated using this allometric equation was almost identical to the observed value (102%, Fig. 5). Thus, we have no indication of a lower BMR in this subterranean species compared to closely related non-subterranean species, given T_a .

Three non-exclusive hypotheses have been proposed to explain the decreased energetic metabolism of subterranean rodents. Is our finding of unreduced BMR in *P. schaposchnikowi* compatible with each of them?

The “cost-of-burrowing hypothesis” states that a reduced mass-independent BMR may compensate the extremely high energy expenditure of digging during foraging activities

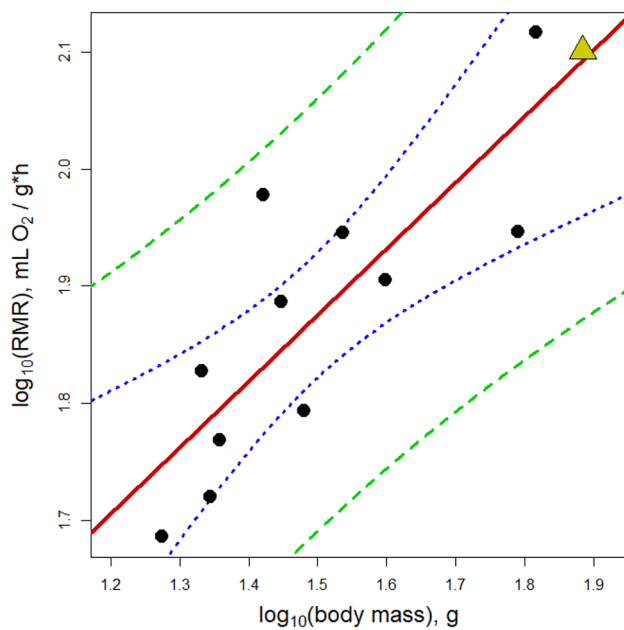


Fig. 5 Scaling of basal metabolic rate to body mass in voles inhabiting the areas with T_{ma} close to that in *Prometheomys schaposchnikowi* locality (Table S2, Online Resource 2). Value for the long-clawed vole (not included in the regression analysis) is depicted by a yellow triangle. Blue dotted and green dashed lines indicate 95% confidence and prediction intervals of the regression, respectively

(Vleck 1979). Under this hypothesis, a subterranean species, which does not show a decrease in BMR, is expected to maintain energy balance by reducing some other energetic expenditures such as reproductive and/or immune response costs (Sheldon and Verhulst 1996; Lochmiller and Deerenberg 2000; Lee 2006). The extremely slow growth and development shown for LCV seems to indirectly support this expectation, whereas the prediction of reduced immune response remains to be tested in the future.

The “respiratory stress hypothesis” (Darden 1972; Arieli 1979) and the “thermal-stress hypothesis” (McNab 1966) both relate the low BMR of subterranean rodents to the physical microenvironmental conditions (hypoxic and hypercapnic or hyperthermic, respectively) in tunnels. Burrow atmosphere and microclimate strongly depend on soil characteristics (Burda et al. 2007; Šumbera 2019). The soil of subalpine meadows of the Caucasus is rather light and often filled with stones which should increase gas diffusion. On the other hand, the soil remains wet for most of the year, which affects the gas permeability in the opposite direction (Arieli 1979). As for thermal stress, LCV may not experience it for most of the year due to the cool high altitude climate, but in summer, daytime temperatures near surface can exceed 25 °C (Akhalkatsi et al. 2006), and overheating seems to be as probable in this voles as in

many other subterranean rodents. In addition, high digging activity itself should lead to increase in CO_2 concentration and temperatures in burrow (Burda et al. 2007). Therefore, within the framework of “thermal-stress” and “respiratory stress” hypotheses, an “aberrant” subterranean rodent with high BMR should exhibit some ecological or behavioral peculiarities, which allow it to avoid overheating and deal with a problem of gas exchange. There are at least two such features in the LCV. First, unlike most truly subterranean rodents that forage primarily underground (but see Tomotani et al. 2012 for *Ctenomys*), LCV expose themselves above-ground very often. Rather than venturing onto the surface, a feeding animal sticks his head out of the hole and picks up plants located just around the burrow opening to drag them inside and eat in safety. Second, foraging tunnels of this species are characterized by a unique, to our knowledge, feature: they are almost twice as wide as one would expect for a rodent of this size (7–8 cm in diameter—Vorontsov 1966; Smorkatcheva unpublished). The larger diameter than necessary based on the size of the animal should be costly in terms of vulnerability to predators as well as energy expenditure on excavating and maintenance. Thus, we speculate that oversizing of tunnels in LCV might be an adaptation preventing respiratory and, in warm weather, thermal stress that would otherwise result from a metabolic rate too high for underground existence.

To conclude, *P. schaposchnikowi* is similar to other subterranean rodents in its slow growth and development, but unlike them does not exhibit the reduced energetic metabolism. This unusual combination of traits along with some behavioral features apparently constitutes the elements of the unique adaptive complex of the relatively small, strictly herbivorous subterranean rodent living in cold humid habitats. Taken together, these characteristics provide indirect support for each of the three hypotheses about the ultimate causes of low BMR in other subterranean rodents.

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Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

Ethics approval All procedures performed in this study were in accordance with the ethical standards of the institutional research committees. The study was approved by the Bioethics Committees of the ZIN RAS #2018–144 and SPbU #131–03-2.

References

- Abramson NI, Lebedev VS, Tesakov AS, Bannikova AA (2009) Supraspecies relationships in the subfamily Arvicolinae (Rodentia, Cricetidae): an unexpected result of nuclear gene analysis. *Mol Biol* 43:1–14
- Abramson NI, Bodrov SY, Bondareva OV, Genelt-Yanovskiy EA, Petrova TV (2021) A mitochondrial genome phylogeny of voles and lemmings (Rodentia: Arvicolinae): evolutionary and taxonomic implications. *PLOS ONE* 16(11):e0248198. <https://doi.org/10.1371/journal.pone.0248198>
- Akhalkatsi M, Abdaladze O, Nakhutsrishvili G, Smith WK (2006) Facilitation of seedling microsites by *Rhododendron caucasicum* extends the *Betula litwinowii* Alpine Treeline, Caucasus Mountains, Republic of Georgia. *Arct Antarct Alp Res* 38:481–488
- Arieli CA (1979) The atmospheric environment of fossorial mole rat (*Spalax ehrenbergi*): effect of season, soil texture, rain, temperature and activity. *Comp Biochem Physiol A* 63:569–575
- Bashenina NV (1975) Guidelines for keeping and breeding new species of small rodents in laboratory practice. Izdatel'stvo MGU, Moscow (in Russian)
- Begall S, Burda H, Gallardo MH (1999) Reproduction, postnatal development, and growth of social coruros, *Spalacopus cyanus* (Rodentia: Octodontidae), from Chile. *J Mamm* 80:210–217. <https://doi.org/10.2307/1383221>
- Begall S, Burda H, Schleich CE (2007) Subterranean rodents: news from underground. Springer, Berlin
- Bennett NC, Jarvis JUM, Aguilar GH, Mc Daid EJ (1991) Growth and development in six species of African mole-rats (Rodentia: Bathyergidae). *J Zool* 225:13–26
- Bennett NC, Faulkes CG, Molteno AJ (2000) Reproduction in subterranean rodents. In: Lacey EA, Cameron G, Patton JL (eds) Life underground: the biology of subterranean rodents. The University of Chicago Press, Chicago, pp 145–177
- Bondareva O, Genelt-Yanovskiy E, Petrova T, Bodrov S, Smorkatcheva A, Abramson N (2021) Signatures of adaptation in mitochondrial genomes of Palearctic subterranean voles (Arvicolinae, Rodentia). *Genes* 12:1945. <https://doi.org/10.3390/genes12121945>
- Bozinovic FT, Carter MJ, Ebensperger LA (2005) A test of the thermal-stress and the cost-of-burrowing hypotheses among populations of the subterranean rodent *Spalacopus cyanus*. *Comp Biochem Physiol, Part A* 140:329–336
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Buffenstein R (2000) Ecophysiological responses of subterranean rodents to underground habitats. In: Lacey EA, Cameron G, Patton JL (eds) Life underground: the biology of subterranean rodents. The University of Chicago Press, Chicago, pp 62–110
- Bukhnikashvili A, Kandaurov A (1998) Threatened and insufficiently studied species (Insectivora, Rodentia). Institute of Zoology of Georgia, Tbilisi
- Burda H (1989) Relationships among rodent taxa as indicated by reproductive-biology. *Z Zool Syst Evolutionsforsch* 27:49–57
- Burda H, Šumbera R, Begall S (2007) Microclimate in burrows of subterranean rodents - revisited. In: Begall S, Burda H, Schleich CE (eds) Subterranean rodents: news from underground. Springer-Verlag, Berlin, pp 20–33
- Busch C, Antinuchi CD, del Valle JC, Kittlein MJ, Malizia AI, Vassallo AI, Zenuto RR (2000) Population ecology of subterranean rodents. In: Lacey EA, Cameron G, Patton JL (eds) Life underground: the biology of subterranean rodents. The University of Chicago Press, Chicago, pp 183–226
- Bushuev A, Tolstenkov O, Zubkova E, Solovyeva E, Kerimov A (2018) Basal metabolic rate in free-living tropical birds: the influence of phylogenetic, behavioral, and ecological factors. *Curr Zool* 64:33–43
- Bushuev A, Zubkova E, Tolstenkov O, Kerimov A (2021) Basal metabolic rate in free-ranging tropical birds lacks long-term repeatability and is influenced by ambient temperature. *J Exp Zool Part A: Ecol Integr Physiol* 335:668–677
- Camín S (2010) Gestation, maternal behaviour, growth and development in the subterranean caviomorph rodent *Ctenomys mendocinus* (Rodentia, Hystricognathi, Ctenomyidae). *Anim Biol* 60:79–95. <https://doi.org/10.1163/157075610X12610595764255>
- Coady JW (1975) Bioenergetics of the brown lemming (*Lemmus sibiricus*). PhD dissertation, University of Alaska, Fairbanks
- Dammhahn M, Dingemans NJ, Niemelä PT, Réale D (2018) Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. *Behav Ecol Sociobiol* 72:62
- Darden TR (1972) Respiratory adaptations of a fossorial mammal, the pocket gopher (*Thomomys bottae*). *J Comp Physiol A* 78:121–137
- Dobson FS, Oli MK (2007) Fast and slow life histories of mammals. *Ecoscience* 14:292–299
- Drożdż A, Górecki A, Grodziński W, Pelikán J (1971) Bioenergetics of water voles (*Arvicola terrestris* L.) from southern Moravia. *Ann Zool Fenn* 8:97–103
- Elizbarashvili ESh, Urushadze TF, Elizbarashvili ME, Elizbarashvili ShE, Schaefer MK (2010) Temperature regime of some soil types in Georgia. *Euras Soil Sci* 43:427–435
- Evdokimov NG (2001) Population ecology of the mole-vole. Izdatel'stvo Ekatherinburg, Ekatherinburg (in Russian)
- Fernández-Salvador R, García-Perea R, Ventura J (2001) Reproduction and postnatal growth of the Cabrera vole, *Microtus cabrerae*, in captivity. *Can J Zool* 79:2080–2085
- Fristoe TS, Burger JR, Balk MA, Khaliq I, Hof C, Brown JH (2015) Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals. *Proc Natl Acad Sci USA* 112:15934–15939
- Gaillard J-M, Yoccoz NG, Lebreton J, Bonenfant C, Devillard S, Loison A, Pontier D, Allaine D (2005) Generation time: a reliable metric to measure life-history variation among mammalian populations. *Am Nat* 166:119–123
- Gambaryan PP (2002) Ways of adaptive changes in claws of digging mammals. *Zool Zh* 81:978–990 (in Russian)
- Gambaryan PP, Karapetyan VS, Ayrumyan KA, Kazaryan KG, Mezhlumyan SK (1957) To the ecology of the long-clawed mole vole *Prometheomys schaposchnikovi* Sat. *Mater Study Fauna Armen SSR* 3:5–16 (In Russian)
- Genoud M, Isler K, Martin RD (2018) Comparative analyses of basal rate of metabolism in mammals: data selection does matter. *Biol Rev* 93:404–438
- Glazier DS (2015) Is metabolic rate a universal 'pacemaker' for biological processes? *Biol Rev* 90:377–407
- Gromov IM, Polyakov IYa (1977) Fauna of the USSR. Mammals. 3. Voles (Microtinae). Nauka, Leningrad (In Russian)
- Horrell ND, Perea-Rodriguez JP, Harris BN, Saltzman W (2017) Effects of repeated pup exposure on behavioral, neural, and adrenocortical responses to pups in male California mice (*Peromyscus californicus*). *Horm Behav* 90:56–63

- İbiş O, Selçukc AY, Sacks BN, Yıldız B, Özcan S, Kefelioğlu H, Tez C (2020) Whole mitochondrial genome of long-clawed mole vole (*Prometheomys schaposchnikovi*) from Turkey, with its phylogenetic relationships. *Genomics* 112:3247–3255
- Kaya A, Coşkun Y (2015) Reproduction, postnatal development, and social behavior of *Ellobius lutescens* Thomas, 1897 (Mammalia: Rodentia) in captivity. *Turk J Zool* 39:425–431. <https://doi.org/10.3906/zoo-1401-73>
- Klaassen M, Agrell J, Lindström Å (2002) Metabolic rate and thermal conductance of lemmings from high-arctic Canada Siberia *Comp Physiol B* 172:371–378
- Kryštufek B, Vohralík V (2005) Mammals of Turkey and Cyprus: Rodentia I: Sciuridae, Dipodidae, Gliridae, Arvicolinae. Koper : Zgodovinsko društvo za južno Primorsko : Univerza na Primorskem, Znanstveno-raziskovalno središče, Založba Annales
- Lacey EA, Patton JL, Cameron GN (2000) The biology of subterranean rodents. Life underground. Chicago Univ Press, Chicago
- Lee KA (2006) Linking immune defenses and life history at the levels of the individual and the species. *Integr Comp Biol* 46:1000–1015. <https://doi.org/10.1093/icb/icl049>
- Letitskaya EP (1984) Materials on reproduction and postnatal development of *Ellobius talpinus* (Rodentia, Cricetidae). *Zool Zh* 63:1084–1089 (**in Russian**)
- Lochmiller RL, Deerenberg C (2000) Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* 88:87–98. <https://doi.org/10.1034/j.1600-0706.2000.880110.x>
- Lovegrove BG (2003) The influence of climate on the metabolic rate of small mammals: a slow-fast metabolic continuum. *J Comp Physiol B Biochem Syst Environ Physiol* 173:87–112
- Luna F, Antenucci CD, Bozinovic F (2009) Comparative energetics of the subterranean *Ctenomys* rodents: breaking patterns. *Physiol Biochem Zool* 82:226–235
- Luna F, Naya H, Naya DE (2017) Understanding evolutionary variation in basal metabolic rate: an analysis in subterranean rodents. *Comp Biochem Physiol Part A Molec Integr* 206:87–94
- McNab BK (1966) The metabolism of fossorial rodents: a study of convergence. *Ecology* 47:712–733
- McNab BK (1980) On estimating thermal conductance in endotherms. *Physiol Zool* 53:145–156. <https://doi.org/10.1086/physzool.53.2.30152577>
- McNab BK (1992) The comparative energetics of rigid endothermy: the Arvicolidae. *J Zool* 227:585–606
- Moshkin MP, Novikov E, Petrovski D (2007) Skimping as an adaptive strategy in social fossorial rodents: the mole vole (*Ellobius talpinus*) as an example. In: Begall S, Burda H, Schleich CE (eds) Subterranean rodents: news from underground. Springer-Verlag, Berlin, pp 49–60
- Muggeo VMR (2003) Estimating regression models with unknown break-points. *Stat Med* 22:3055–3071
- Muggeo VMR (2008) Segmented: an R package to fit regression models with broken-line relationships. *R News* 8:20–25
- Muggeo VMR (2016) Testing with a nuisance parameter present only under the alternative: a score-based approach with application to segmented modelling. *J Stat Comp Simul* 86:3059–3067
- Muggeo VMR (2017) Interval estimation for the breakpoint in segmented regression: a smoothed score-based approach. *Austral N Z J Stat* 59:311–322
- Nadeau JH (1985) Ontogeny. In: Tamarin RH (ed) *Biology of new world Microtus*. Spec Publ Am Soc Mammal 8 Boston University Boston, Massachusetts, pp 254–285
- Naya DE, Spangenberg L, Naya H, Bozinovic F (2013) How does evolutionary variation in basal metabolic rates arise? A statistical assessment and a mechanistic model. *Evolution* 67:1463–1476
- Nevo E (1979) Adaptive convergence and divergence of subterranean mammals. *Annu Rev Ecol Syst* 10:269–308. <https://doi.org/10.1146/annurev.es.10.110179.001413>
- Nevo E (1999) Mosaic evolution of subterranean mammals: regression, progression and global convergence. Oxford University Press, Oxford
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 18 Feb 2022
- Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. *Trends Ecol Evol* 17:462–468
- Rosenblatt JS (1967) Nonhormonal basis of maternal behavior in the rat. *Science* 156:1512–1513
- Sheldon BC, Verhulst S (1996) Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends Ecol Evol* 11:317–321
- Sibly RM, Brown JH (2007) Effects of body size and lifestyle on evolution of mammal life histories. *Proc Natl Acad Sci USA* 104:17707–17712. <https://doi.org/10.1073/pnas.0707725104>
- Smorkatcheva AV, Kumaitova AR, Kuprina KV (2016) Make haste slowly: reproduction in the Zaisan mole-vole, *Ellobius Tancrei*. *Can J Zool* 94:155–162
- Spitzenberger F, Steiner HM (1964) *Prometheomys schaposchnikovi* Satunin, 1901, in Nordost-Kleinasien. *Zeitsch Saugietierk* 29:116–124
- Steppan SJ, Schenk JJ (2017) Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. *PLOS ONE* 12:e0183070
- Šumbera R (2019) Thermal biology of a strictly subterranean mammalian family, the African mole-rats (Bathyergidae, Rodentia)—a review. *J Therm Biol* 79:166–189
- Tomotani BM, Flores DEFL, Tachinardi P, Paliza JD, Oda GA et al (2012) Field and laboratory studies provide insights into the meaning of day-time activity in a subterranean rodent (*Ctenomys aff. knighti*), the tuco-tuco. *PLOS ONE* 7:e37918. <https://doi.org/10.1371/journal.pone.0037918>
- Turov SS (1926) To the biology and spreading of *Prometheomys schaposchnikovi* Sat. *Byull Sci Inst Explor Reg Cauc Nord* 1:23–30 (**In Russian**)
- Vereshchagin NK (1959) The mammals of the Caucasus; a history of the evolution of the fauna. (Mlekopitayushchie Kavkaza; Istoriya Formirovaniya Fauny). Publ Acad Nauk USSR, Jerusalem (**in Russian**)
- Vleck D (1979) The energy cost of burrowing by the pocket gopher, *Thomomys bottae*. *Physiol Zool* 52:122–136
- Vorontsov NN (1966) New data on the biology and taxonomic position of *Prometheomys schaposchnikovi* Satunin. *Zool Zh* 45:619–623 (**In Russian**)
- White CR (2003) The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals. *Physiol Biochem Zool* 76:122–134
- Yatsenko EN (1959) Reproduction of the vole *Prometheomys schaposchnikovi* Satunin. *Zool Zh* 38:916–991 (**in Russian**)
- Zimina RP, Yasny EV (1977) Observations on the ecology of the long-clawed mole vole. *Byull MOIP Otd Biol* 2:24–30 (**in Russian**)
- Zullinger EM, Ricklefs RE, Redford KH, Mace GM (1984) Fitting sigmoidal equations to mammalian growth curves. *J Mamm* 65:607–636

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