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Biology of reproduction and postnatal development of a little-studied Schelkovnikov's pine vole *Microtus schelkovnikovi* Satunin, 1907 (Rodentia, Arvicolinae)

Tanya A. Zorenko

ABSTRACT. Schelkovnikov's pine vole *Microtus schelkovnikovi* is a little-studied endemic species of the Talysh-Western Alborz Mountains, covered with relict Hyrcanian broad-leaved forests. Laboratory studies have shown the seasonality of reproduction in the species. *M. schelkovnikovi* voles have low breeding intensity and small litters, however maintain long-term reproductive activity. Social monogamy is a characteristic of the species under laboratory conditions. Most of the predictions of monogamy are found in *M. schelkovnikovi*: females mating only within formed pairs, prolonged courtship, small litters, small testes and a low number of ejaculations in males. The copulatory stereotype in *M. schelkovnikovi* is characterized by a low number of ejaculations, triggered by numerous intromissions and an average level of genital stimulation. The pattern of copulatory stereotype unites the Schelkovnikov's pine vole with species of such taxa as *Microtus* s. str., *Sumeriomy*s, and *Terricola*, which corresponds to distinguishing the West Palearctic branch of voles in the tribe Arvicolini and opposes the East Asian branch identified on the basis of molecular studies.

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Tanya Zorenko [tatjana.zorenko@lu.lv], Department of Zoology and Animal Ecology, Faculty of Natural Sciences, University of Latvia, LV-1004, Riga, Latvia.

Биология размножения и постнатальное развитие малоизученной полевки Шелковникова *Microtus schelkovnikovi* Satunin, 1907 (Rodentia, Arvicolinae)

Т.А. Зоренко

РЕЗЮМЕ. Полевка Шелковникова, *Microtus schelkovnikovi* — малоизученный эндемичный вид в горах Талыша и западного Эльбурса, которые покрыты реликтовым Гирканским широколиственным лесом. Лабораторные исследования показали сезонность размножения вида. Для *M. schelkovnikovi* характерны низкая интенсивность размножения и маленькие выводки, но животные сохраняют долгую репродуктивную активность. Для вида в лабораторных условиях характерна социальная моногамия. Большинство показателей, предсказывающих моногамию, обнаружены у M. *schelkovnikovi*, а именно, спаривание происходит только с самцом из своей пары, продолжительное ухаживание, небольшие выводки, относительно мелкие семенники и небольшое число эякуляций. Стереотип спаривания *M. schelkovnikovi* характеризуется небольшим числом эякуляций, которые достигаются большим числом интромиссий и средним уровнем генитальной стимуляции. Специфика спаривания объединяет *M. schelkovnikovi* с видами таких таксонов, как *Microtus* s. str., *Sumeriomys* и *Terricola*, что соответствует выделению западно-палеарктической группы полевок трибы Arvicolini и противостоит восточноазиатской группе, что подтверждает данные, полученные на основании молекулярных исследований.

КЛЮЧЕВЫЕ СЛОВА: Полевка Шелковникова, *Microtus schelkovnikovi*, стереотип спаривания, социальное поведение, постнатальное развитие, стратегия размножения, моногамия.

Introduction

The Schelkovnikov's vole, *Microtus schelkovnikovi* Satunin, 1907 is endemic to the Talysh-Western Alborz Mountains covered by relict Hyrcanian broad-leaved forests and inhabits humid forests (Steiner, 1972; Gromov & Polyakov, 1992). The species lives in the Lankaran region of south-eastern Azerbaijan (Khatukhov & Tembotov, 1982) and in the Provinces of Gilan and Mazandaran in the Kuramobad region of northern Iran (Steiner, 1972; Nadachowski, 2007). The range of *M. schelkovnikovi* is small and measures 9360 km^2 with the elevational range being 27–1970 m (Kryštufek & Shenbrot, 2022). Within the Hyrcanian biogeographical province, precipitation decreases from west to east, while mean annual temperature increases in the same direction (Zazanashvili *et al*., 2020). Therefore, the summer dry season in Iran is much longer than in Azerbaijan. The average annual temperature during the day is 16.9°C and 8°C at night. Average monthly maximum (July and August) and minimum (January) temperatures are 28°C and 2.5–3.0°C, respectively. Around 70–60% of atmospheric precipitation falls in spring, autumn and winter, and summers are dry. These climatic fluctuations affect the vegetation and food supply of voles.

The species was described in 1907 by Satunin as *Microtus schelkovnikovi* based on a single specimen from Lankaran district, which was caught in the forest near the village of Dzhi (Ognev, 1950). Initially, Shidlovsky (1941) considered the Schelkovnikov's vole to be subspecies of the pine vole *Pytymys majori* Thomas, 1906, however later defined it as a separate species from Talysh (Shidlovsky, 1976). This point of view was supported by Ognev (1950). According to another opinion, the specimens belonged to Caucasian subspecies of the pine vole *Pytymys subterraneus schelkovnikovi* (Ellerman & Morrison-Scott, 1951). Many authors believed that *M. schelkovnikovi* was a representative of the endemic Ponto-Caucasian group of pine voles, where it occupied a special position (Khatukhov & Tembotov, 1982; Tembotov, 1983; Akhverdyan *et al*., 1992). Gromov assigned the Schelkovnikov's vole to the subgenus *Terricola* within the genus *Microtus* (Gromov & Polyakov, 1992).

A comparison of morphological and karyological characters made it possible to establish that *M. schelkovnikovi* does not belong to the subgenus (Kryštufek & Shenbrot, 2022) or genus (Abramson *et al*., 2021) of pine voles *Terricola*, but is the only representative of the independent subgenus *Hyrcanicola* within the genus *Microtus*, *M.* (*Hyrcanicola*) *schelkovnikovi* (Nadachowski, 2007).

Indeed, the chromosome set of *M. schelkovnikovi* differs noticeably from other species of pine voles, being the most primitive. The number of chromosomes in the karyotype is $2n = 54$, NF = 62 (Ivanov & Tembotov, 1972; Kuliev & Kuliev, 1978; Akhverdyan *et al*., 1992; Kuliev & Bickham, 2010). Morphologically, *M. schelkovnikovi* differs from pine and common voles in many exterior features: it has a thick and very short velvety pelage, small ears and a short distinctly bicolored tail, which composes 19–23% of body length (Alekperov, 1959; Steiner, 1972; personal observation) and four pairs of nipples (Shidlovsky, 1941; Kratochvil, 1970). The species is clearly distinguished by the first lower molar m1. The skull is short and wide, the greatest length of the skull is 23.0–25.3 (mean 23.9) mm. Nasals are comparatively short, and the interorbital region is wide and ranges between 4.3–4.7 mm. The brain capsule is wide and high; the greatest height is noted at the level of a third upper molar (Khatukhov & Tembotov, 1982). Incisors and molars are comparatively small (Gromov & Polyakov, 1992). In general, the Iranian specimens are slightly larger than Azerbaijani individuals (Steiner, 1972).

The ecology of the species remains understudied. Some data on *M. schelkovnikovi* vole's ecology in nature can be found in the study of Khatukhov and Tembotov (1982). In Talysh and Alborz, *M. schelkovnikovi* lives in lowland deciduous forests. Forests in the lower altitudes are represented by a number of relict Arctic-Tertiary thermophilic species, such as ironwood (*Parrotia persica*), Caspian locust (*Gleditsia caspica*), chestnut-leaved oak (*Quercus castaneifolia*), Caucasian zelkova (*Zelkova carpinifolia*) and others. The vole is also found in moist beech, beech-hornbeam forests with an admixture or predominance of relict species of ironwood and chestnut-leaved oak in some habitats. Voles occupy slopes and gorges overgrown with shrubs, ferns, and mosses (Kadatsky, 1964). The lower layer of the forest is represented mainly by dead and dry leaves during the dry period of the year from May to September, when there is very little precipitation (about 25% of the annual norm). In spring and early autumn some habitats in Iran are dominated by grasses and cereals (Akhani *et al*., 2010).

The first attempt to combine the available information about *M. schelkovnikovi* was made in the 90s in the project "Rodents of the former USSR. Status assessment and action plan for environmental protection" (Zorenko, 2001). In addition, the species was considered within the framework of complex studies on play behaviour (Zorenko & Andersone, 1996) and exploratory behaviour (Zorenko *et al*., 1989). The description of vocalization in voles revealed significant differences between *M. schelkovnikovi* and *Terricola daghestanicus* Schidlovsky, 1919 (Rutovskaya, 2015). The lack of descriptive data on the ecology and behaviour may be due to the fact that the species inhabits a small range, located in a region inaccessible to researchers. In addition, *M. schelkovnikovi* voles are difficult to breed in captivity (personal communication with Nikolay Vorontsov).

The purpose of this work was to study the features of biology in *M. schelkovnikovi* under laboratory conditions, such as: vole reproduction (i), formation of exterior features and stereotypies of everyday and social behaviour in early postnatal ontogenesis (ii), copulatory stereotype of *M. schelkovnikovi* in comparison with other vole species of the tribe Arvicolini (iii) and to determine the type of reproductive strategy of *M. schelkovnikovi* according to the obtained behavioural results (iv). In addition, the existing data on ecology were analysed, since any information about this little-studied species may be useful.

Material and methods

Model object and experiment design

Schelkovnikov's pine vole laboratory population founders (five males and four females) were sampled in the forest belt of the Talysh Mts. (Azerbaijan, Lerik region, 18 km to Shovu; N38.72°, E48.7°) and brought to the University of Latvia in June 1988. This study is based on data obtained in 1988–1994. Research was carried out on wild animals and animals of the first and second generations in the Laboratory of Ethology. All applicable international, national, and/or institutional guidelines for the care and use of animals for investigations were respected (Guillén, 2017).

The founder voles were placed individually in standard cages (450×200×150 mm) for 10 days. Then four pairs were formed: 2- to 3-month-old males and females were housed in glass terrarium (700×350×400 mm) containing about 7 cm of substrate and provided with a plastic box (150×150×150 mm) and two tunnels (200×50×50 mm). Three pairs were observed for 4 months, and one for 7 months. Observations were carried out for three days from the onset of the experiment and included the recording of their behaviour (three hours on the first day; and later two hours a day). The female was checked for the phase of the oestrus cycle once a week, according to the method described previously (Zorenko & Skinderskaya, 1996). F1–F2 animals were paired and observed for 6 months (one pair for 12 months). Unrelated specimens were selected from different pairs of wild voles to avoid inbreeding. During the experiment, the following reproduction indicators were recorded: the period from the pair formation to the first birth (in days), the number of births and the number of pups survived until the 20th day.

Due to low reproductive activity, pairs were formed in four instalments: at the end of August (7 pairs), November (5 pairs), January (7 pairs), and April (2); a total 21 pairs. The study aimed to reveal the influence of the season on reproduction.

Three groups consisting of two males and two females were formed in the spring of 1991. The experiment involved F1 voles born in the autumn. Animals were marked by shearing wool. Before the start of the experiment, the voles were kept singly for two days; females were in the proestrus phase. Observation in the first three days was carried out for 6 hours to determine the first attack and the number of attacks per three hours. The vole was considered "dead" and removed from the experimental cage, if a loss of body mass and the life-threatening bite marks on the body were noted upon weighing. Data regarding avoidance of contact between individuals, the manifestation of aggression and "killing", as well as the first episode of crowding and onset of nest construction were collected during the experiment.

In the autumn of 1992, four pairs of related individuals (brother and sister) were formed to determine the effect of inbreeding on reproduction. Voles were separated for two months and perceived each other as strangers. Pairs were observed for 6 months according to the same scheme as pairs of unrelated individuals; reproduction rates were recorded.

A mixture of sawdust and wood shavings was used as a substrate, and hay was served as nesting material. Carrots, apples, a mixture of grain, cereals and hay formed the diet. In spring and summer, animals received grass (the leaves of *Taraxacum officinale* and *Trifollium* sp.). The temperature in the laboratory was maintained at 20 ± 2°C and the lightning mode was 12 hours of light and 12 hours of darkness. Toilet areas were cleaned twice a week, while full cleaning was carried out once every two weeks in the summer and once a month in other seasons.

Studying of the growth and rate of individual development

The pups were examined daily (until the 20th day after birth). The body mass (g), body length (from the most oral point of rostrum to base of tail, mm), tail length (centre of the anus — tip of the tail, not counting hair, mm), the length of the hind legs (tip of third toe, without claw — the most prominent point of heel joint, mm) and the ear length (proximal edge of *incissura intertragica* — distal edge of the ear, mm) were measured. The days of the ear formation outset, the eruption of incisors, the divergence of fingers on extremities and the opening of the eyes were accounted. In total, 21 pairs produced 43 litters. Seven of those were obtained from the wild-born pairs, and 36 — from voles of the first and second laboratory generations.

Social behaviour on neutral territory

In the spring of 1991, the animals were housed individually in cages (400×200×150 mm) for two days. An experimental glass cage (700×360×400 mm) was divided into two compartments by an opaque plastic partition. Animals were marked by cutting hair on different parts of the body, and then a single specimen was placed in each compartment. The voles had to explore the new space for 5 minutes. Then the partition was removed, and observations continued for another 10 min. Eighteen experiments were carried out on 15 males at the age of 3 months, and 20 experiments were performed on 12 males and 12 females (in proestrus phase) at the age of 3–4 months. Seven 7- to 9-month-old males and seven females were euthanized by cervical dislocation. The length (mm) and mass (mg) of the testes and vesicular glands in males and the length and width of the vagina and cervix uteri (mm) in females were measured.

Copulatory behaviour

Usually, the experiments were performed in neutral territory (Zorenko & Malygin, 1984). Since unfamiliar *M. schelkovnikovi* individuals refused to mate in neutral territory, the design of the experiment had to be changed. The formed pairs were separated, and male was placed in an individual cage (400x350x200 mm). When the oestrus stage was detected in the female (Zorenko & Skinderskaya, 1996), the male was returned to the territory of the female. Experiments on sexual behaviour were carried out according to the standard method described in detail in early publications (Zorenko & Malygin, 1984; Zorenko & Atanasov, 2018). For the copulatory stage, the following indices were recorded: *Latency* (L, s) — period from introduction of the male in the territory of the female until the first intromission; *Intromission Frequency* (IF) — number of mounts with intromissions within a copulatory series, not including mount ending with ejaculation; *Mean number of thrusts per intromission* (T/I 1st series); *Number of thrusts per Ejaculation* (T/E 1st series) — number of thrusts during mount ending with ejaculation; *Total Number of Thrusts* (NT 1st series) — total number of thrusts during mounts with intromission and ejaculation in a series; *Duration of Copulation* (DC) — time interval from the first intromission of a series to the end of ejaculation; *Postejaculatory Interval* (PEI) — interval from the end of an ejaculation until the beginning of the next intromission; *Ejaculation Frequency* (EF) — total number of ejaculations; ΣIF — total number of intromissions during the whole copulatory period and ΣNT — total number of thrusts during a mount with intromission and ejaculation during all the series.

In addition, similar experiments were carried out on *M. obscurus* Eversmann, 1841 (Azerbaijan, Lerik region, Shovu Village, meadow habitats at an altitude of 1400 m above sea level; in 1988) and *T. daghestanicus* (Ossetia, Alagir District, Tsei Gorge; N42.80°, E43.93°; in 1987). According to the general scheme, 15 experiments were carried out with *M. schelkovnikovi* and 10 experiments each with *T. daghestanicus* and *M. obscurus*.

Descriptive statistics were obtained in Microsoft Excel 2010. Average values and standard errors were calculated and compared using the Student's t-test. In all statistical comparisons, the level of significance was $p < 0.05$. The text indicates the number of animals (n), mean and standard deviation ($X \pm SD$).

Results

Ecology

Ironwood dominated in the studied habitat, herbaceous vegetation was absent, and the space under the trees was covered with dry foliage. Over three days (June 13–15) on the area of 800 sq. m 25 animals were captured, including 3 adult males and 3 females (sex ratio 1:1) as well as young animals: 10 males and 5 females (sex ratio 2:1). The number of voles was 3.3% per 100 trap-days.

Based on the gestation period and age of the young voles, reproduction should have begun in late February-early March. Daily activity was the highest in the morning (7.00–10.00; 75% of animals) and evening (25%). Digging activity and soil ejections from the burrows were not observed. Runway passages were located under dead leaves at a depth of about 3–5 cm, mainly along the roots of trees. Surface movement paths were not typical for this species.

In the studied habitat, *M. schelkovnikovi* vole was the dominant species, since no other species were recorded during the three-day capture period. The voles were active outside their burrows, moving along dry foliage. On the first day of observations between 17:00 and 20:00, five episodes of vocalization were recorded, and four — on the second day. Two young males were caught during the described observation period.

Seasonality of breeding

Under laboratory conditions, *M. schelkovnikovi* reproduced all year round, but with unequal intensity in different seasons. The largest number of litters and offspring was recorded from February to May (22 litters) and from September to December (16 litters). Only single litters were recorded in June–August (3 litters) and in December–January (2 litters) (Fig. 1). Autumn and spring, including February, accounted for 88% of all litters and pups. During these months, females were most successful at weaning; offspring survival was the highest (84%) in spring, followed by 38% in the autumn. Observations showed that females after giving several litters usually had a latent period when reproduction did not occur. If the voles were paired at the end of August, the offspring were born between September and December, with a following pause in reproduction, and new litters were born only the next spring. If pair formation took place in January, the voles reproduced mainly in the spring, however in the autumn they could bring one more litter. The single pair that bred for 12 months gave birth to three litters in the autumn, to two litters both in February and May, and finally had two more autumn litters after summer break.

Duration of pregnancy and birth intervals

Over five years, 21 mature females produced 43 litters and 123 pups. Most often, a female had only one litter (55%); two and three litters were observed in 23% and 14% of females, respectively. Four litters were recorded in 4% females, and seven litters were born from a single female. The interval between parturitions averaged 59.8 ($n = 22$; SD = 34.9) days. The result was affected by winter and summer reproduction breaks. The gestation period varied from 21 to 23 days. Postpartum mating was common, but did not always result in pregnancy, as evidenced by the long interval between births. Only one vole pair produced litters in 21–25 days; however, this was due to total mortality in many litters.

Young voles started breeding late, not earlier than reaching 5 months of age; apparently, due to the pres-

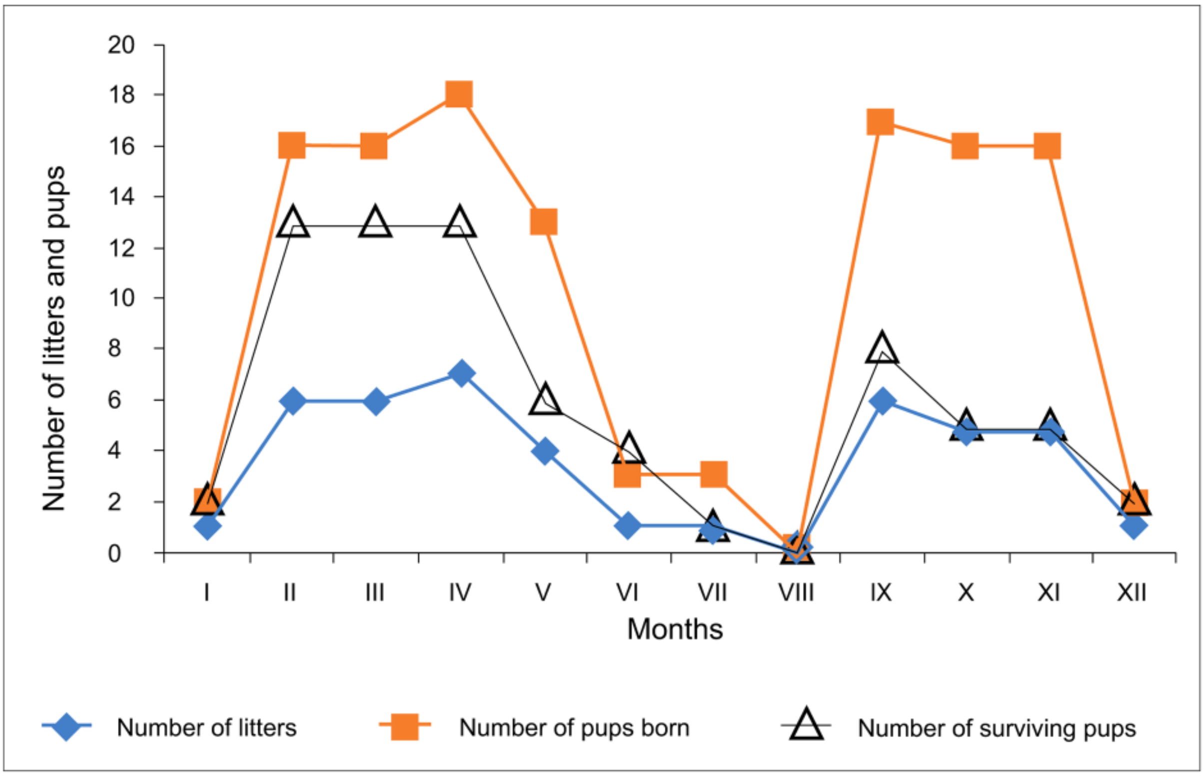

Fig. 1. Influence of the season on the number of litters, the number of pups born and successfully reared pups.

ence of the reproduction pause. The voles of the spring generation began to breed in the autumn, while voles of the autumn generation — only starting with February–March. However, voles retained the ability to keep long-term reproductive pace: females — up to 20 months (*n* = 15; 13 ± 7) and males — up to 24 (*n* = 15; 15 ± 7) months.

Litter size ranged from 1 to 4 pups with a mean of 2.86 (± 0.85). Only one of 43 litters had one pup (2%); 81% of litters had 2–3 pups and 17% of litters had 4 pups. Litters of wild-caught parents consisted of 2–4 pups (*n* = 7; 3.0 ± 0.82) with 25% mortality rate. In pairs of F1–F2 individuals, litter size did not differ (*n* = 26; 2.8 ± 0.80), while the mortality of pups increased to 34%.

Inbreeding tolerance

The interval between the beginning of pair formation and the birth of offspring was 25–38 days (*n* = 4; 30.2 ± 5.5). The litter size was not different from outbred voles (*n* = 11; 2.9 ± 0.3). Infant mortality was high; overall, 9 out of 11 pups died after 15 days and the rest after 30 days. Three pairs stopped breeding after the death of the first litter, and one pair gave birth to 20 pups (7 litters) over 12 months, but 12 of them died by the 15th day, and three by the 30th day. Only 25% of the offspring of this pair survived. Overall, the offspring mortality rate in inbred pairs was 70%.

The size of genitals

During the breeding season, the length of the testes was 5–6 (*n* = 7; 5.5 ± 0.32) mm, and mass was 46–93 (*n* = 7; 65.9 ± 19.6) mg. The seminal vesicles were extremely small; their mass did not exceed 25 (*n* = 7; 20.0 ± 4.28) mg. The length of the vagina in females ranged from 5 to 7 (*n* = 7; 6.4 ± 0.90) mm. Index of the relative size of the testes (ratio of the length of the right testis to the length of the head and body) was 0.059. The length of the cervix uteri was 1.4–2.0 (1.6 ± 0.3) mm, and the width was 1.3–1.5 (1.3 ± 0.2) mm. In the experienced female after several litters, the width of the cervix uteri increased to 1.7 mm. The head of the glans penis was measured in three males. Its average length was 3 mm, and its relative diameter (ratio of length to width) was 70.8. The central process of the glans penis was well developed and protruded from the crater, while the lateral processes were developed poorly. Hip and flank glands were not found. Males marked a territory with urine, leaving streaks on the substrate, and, possibly, with anal gland secretion, since males often pressed the anal region of the body to the ground and pulled it along the substrate.

Postnatal ontogenesis

In the first hours of life, neonates had a red skin colour. The dark pigment appeared only by the end of the first day. By the 3rd day, the dorsal side of the body got

Table 1. Measurements of exterior characteristics of young voles *Microtus schelkovnikovi* in postnatal ontogenesis. Statistical information is presented as follows: arithmetic mean ± standard error. Abbreviations: M — body mass (g); L — body length (mm); Pl — hind foot length (mm); C — tail length (mm), Au — ear length (mm); n — a number of observations.

Age, days	Signs	Measurement, mm	*n*	Age, days	Signs	Measurement, mm	*n*
1	M	2.5 ± 0.05	25	20	M	13.3 ± 0.53	20
	L	35.3 ± 0.12			L	72.8 ± 1.12	
	Pl	5.4 ± 0.11			Pl	14.1 ± 0.11	
	C	5.4 ± 0.10			C	15.9 ± 0.32	
					Au	6.3 ± 0.11	
5	M	4.5 ± 0.11	25	25	M	13.8 ± 1.10	10
	L	44.3 ± 0.60			L	76.0 ± 2.09	
	Pl	7.6 ± 0.13			Pl	15.1 ± 0.14	
	C	7.7 ± 0.14			C	18.1 ± 0.80	
	Au	2.0 ± 0.10			Au	7.2 ± 0.20	
10	M	6.9 ± 0.12	25	30	M	17.2 ± 0.32	10
	L	52.4 ± 0.86			L	78.5 ± 0.61	
	Pl	10.5 ± 0.41			Pl	15.5 ± 0.22	
	C	10.4 ± 0.25			C	20.0 ± 0.37	
	Au	4.0 ± 0.23			Au	7.1 ± 0.20	
15	M	8.7 ± 0.22	25	60	M	20.4 ± 0.58	10
	L	62.0 ± 0.70			L	91.1 ± 0.87	
	Pl	12.8 ± 0.17			Pl	15.5 ± 0.22	
	C	13.4 ± 0.18			C	20.2 ± 0.37	
	Au	5.3 ± 0.12			Au	7.2 ± 0.12	
120 males	M	24.6 ± 0.80	7	120 females	M	23.4 ± 1.28	7
	L	93.5 ± 0.55			L	92.5 ± 0.66	
	Pl	15.5 ± 0.24			Pl	15.3 ± 0.25	
	C	23.5 ± 0.60			C	23.8 ± 0.63	
	Au	7.5 ± 0.50			Au	7.3 ± 0.51	

Table 2. Development of the exterior morphological characteristics of *Microtus schelkovnikovi* pups in comparison with *Terricola majori* and *T. subterraneus* in the early postnatal period of ontogenesis. Statistical information is presented as follows: arithmetic mean ± standard error, range in parentheses.

Character examined	*M. schelkovnikovi*	*T. majori* Mambetov, 1987	*T. subterraneus* Zimová, 1987
Ear formation, days	5.4 ± 0.10 (4–6)	2.4 ± 0.06 (2–4)	4
Cutting of lower incisors, days	6.4 ± 0.08 (6–7)	4.6 ± 0.10 (3–6)	5
Cutting of upper incisors, days	7.9 ± 0.10 (7–9)	5.4 ± 0.14 (4–7)	7
Divergence of fingers on forelimbs, days	8.4 ± 0.14 (7–10)	7.5 ± 0.08 (7–10)	(9–10)
Divergence of fingers on hind foot, days	10.1 ± 0.13 (8–12)	9.6 ± 0.09 (9–13)	(11–14)
Opening of eyes, days	12.8 ± 0.13 (11–15)	8.7 ± 0.13 (7–11)	11

covered with fluff and with dark short fur a day later. On the 4–5th day, fluff first appeared on the abdominal side and limbs, and fur appeared after another day. On the 9th day, the juvenile voles had almost complete fur cover.

The formation of earlobes is a long process and takes at least four days. From the second day after birth, the earlobe directed away from the head and began to move upward at an angle 45–90° and only then turned 180°, completing its full development. The eruption of the lower incisors and the divergence of fingers on forepaws occurred two days earlier than on the upper incisors and on the hind paws (Table 2). Molars began to erupt on the 10th day. Eye opening was observed on average at 12.8 days. The length of the palpebral fissure at 15 days of age was 1.2 mm, and by the 60th day — 1.5 mm.

Pups grew quickly, especially in the first 10 days. Body mass of neonates was 2.2–2.9 g and their body length was 34–36 mm (Table 1). Neonate body mass constituted 20% of the two-month-old voles and 10.4% of four-month-old vole body mass. Body length was 37.8% compared to 4-month-old voles. By the 30th day, their body mass increased by 6.9 times and body length by 2.2 times. At 60 days, the body length was already 98.5% compared to adult animals. The growth of voles slowed down starting with the age of two months, accelerating slightly by the fourth month. Newborns usually were lying on the side, moving their legs. From the 3rd to the 5th day, they began to roll over from their back to their belly. On the 6th day, once the muscles of the neck and back strengthened, they were able to rise and hold their head. On the 7th–8th day, the pups started crawling, first slowly, and on the 9th day — quickly.

With the 11th day, the voles transitioned to walking, and on the 12th–13th day they were already running. The eye opening is a turning point in the vole life cycle as they quickly begin to develop basic behaviour patterns. Once the pups opened their eyes, their activity and mobility improved. Comfort behaviour exposed as self-grooming (licking the paws, belly and sides, head rubbing, etc.) appeared on the 10th day of age and fully developed by the 25th day. Starting with the 12th day, the pups first attempted to gnaw solid food with incisors. At first, the voles ate food that was lying on the substrate. On the 20th day, they were already able to hold the food object in their forepaws. At this age, voles started to sniff, gnaw, pull, and turn over objects exploring the natal territory. Along with this, digging appeared (at first only forepaws movements, and later — throwing out the substrate with the hind legs), as well as attempts at nest building. At first, elements such as collecting hay in a certain place, gnawing it into pieces and forming a nest were irregular, but by 38 days of age, voles could build a simplified, sometimes temporal nest, separating from their parents. Social contacts appeared with the 13th day: naso-nasal sniffing; later — sniffing of the anogenital area, following each other and crowding into the nest. Defensive uprights and vocalizations appeared after the 14th–15th day. Play behaviour in this species was weakly expressed and was observed only in a short period from 12th to 21th days.

A female was suckling the young until the 20th day. Males also exhibited parental care: father kept the offspring warm and carried the pups to the nest. Matured offspring coexisted peacefully in the same territory with their parents until the 45th day. Later the male became less tolerant towards his sons (5 episodes of a father attacking his son were recorded). *M. schelkovnikovi* was not accustomed to humans and remained aggressive during the 5 years of observation.

Moulting of juveniles started usually mainly on the 30th day and ended approximately on the 60th day in the following sequence: belly, sides, dorsal side of the body, cranial and caudal parts of the back, medial surface of the limbs. The animals had soft chocolate-coloured backs, a characteristic of adult voles, and the ventral side of their bodies had a distinct ochre-coloured pelage.

Social behaviour

The social behaviour of Schelkovnikov's vole included the elements connected to recognition (sniffing), defensive (escape, upright), ritualized aggressive and open aggressive. When meeting in the neutral arena, males did not approach each other closer than 10 cm; the average number of approaches was 3.4 ± 2.3. Approaches composed 34% (59 out of 171) of all contact types. The sniffing was noted in 6% of cases. However, males left traces of urine and faeces, which were often sniffed by the opponent. Open conflict was rare. During 180-minute observation of 15 males, aggressive acts (biting, fighting and chasing) were recorded only in 4% (7 out of 171). More often, the ritualized aggression was observed in the form of upright threat, confrontations and vocalizations (38%; 67 out of 171), forcing the enemy to interrupt the attack and retreat. Contact avoidance was noted in 16% of cases: voles scattered to opposite corners of the cage, without trying to contact.

When unfamiliar voles of the opposite sex met each other, a clear difference in the behaviour of males and females was observed. A total of 152 behavioural patterns were noted in males and 179 in females. Males sought to maintain contact with females; therefore, they initiated approaching, sniffing, and following a partner (76%), and were significantly less likely to avoid contact (24%). Males never showed any aggression towards females when meeting her, however often marked the territory. In contrast, females demonstrated ritualized patterns of aggression more often, in the form of aggressive uprights, vocalizations, confrontation, and, in rare cases, boxing (all together 55%), and were less likely to maintain contact with males (45%). No acoustic behaviour was noted in males, but squeaking was frequent in females (median 2.5; 2–6 elements per 10-minute experiment).

The introduction of a stranger male into a territory occupied by a pair caused aggression in the resident male. He pursued and attacked the rival male, demonstrated "dancing" movements, and marked the territory by pressing the anogenital region of the body to the substrate. Females did not participate in the defence of the territory.

Voles lived successfully only in pairs. Three attempts to form experimental groups of two males and two females resulted in the dominance of one pair, while two other animals lost body mass and were removed from the experimental cage after 2–3 days to avoid their dying. The dominating pair was formed during the first hour after the onset of the experiment; this pair built a nest in the second hour of observation. Rare attacks and pursuits were observed only between males. The first attack was observed after 3–5 hours (3.7 ± 1.15). Within three hours, 1 to 3 attacks were recorded between males ($n = 3$; 2.0 ± 1.0). "Death" of the male occurred on the 2–3rd day (2.3 ± 0.58), of the female — on the 3–4th (2.3 ± 0.58). The animals were subdued, although there were few bite marks.

Copulation

Behavioural observations of vole pairs in a familiar cage showed that a male usually started courtship, when a female was in a state of proestrus. On this occasion courtship sometimes lasted up to two or three hours with breaks. The male actively followed the female, occasionally with characteristic vocalization (singing) and waltzing (males moved around the female in small steps and attempted to mount). The unreceptive female avoided the male, squeaked repeatedly and did not adopt lordosis position. Conversely, the receptive female performed a stimulating "stroll" in front of the male. The female strolls and the male waltzing promoted the synchronized behaviour in partners leading to mating. Mating occurred only in the formed pairs. The female refused to mate with the unfamiliar male, squeaked and ran away. In our study, the male was temporarily isolated, and then returned to a common territory with the female (see Methods). The male quickly found a receptive female. The behaviour of males included naso-nasal and naso-anal sniffing, following, and waltzing. Singing was rarely recorded in these experiments (3 episodes for all 15 experiments).

The courtship period for 78.6% of pairs lasted between 10 and 30 minutes. Mating included 2–3 series, each series ended with ejaculation. The series included from 4 to 12 intromissions (mounts with vaginal insertion), and T/I varied from 1 to 4 thrusts. The copulatory stereotype is similar in all three species of studied voles, especially in the first mating series (Table 3). However, the probability that the pre-insemination mount included only one thrust is noticeably higher in *M. obscurus* and *M. schelkovnikovi* compared to *T. daghestanicus*. In addition, quantitative differences were manifested in overall mating indices (Σ IF, Σ NT and EF). The lowest number of mating series was noted in *M. schelkovnikovi*, the largest — in *M. obscurus*; consequently, both the number of intromissions (Σ IF) and the level of genital stimulation decreased (Table 3). Statistically significant differences in EF were recorded only between *M. schelkovnikovi* and *M. obscurus* (t = 5.68; $p < 0.001$). On the contrary, the number of intromissions in *M. obscurus* is much higher than in *M. schelkovnikovi* (t = 4.68; $p < 0.001$) and *T. daghestanicus*. The number of thrusts is much greater in *M. obscurus*; it differed significantly from that of *M. schelkovnikovi* (t = 2.79; $p < 0.01$), while with *T. daghestanicus* the differences were not significant ($p > 0.05$). After ejaculation, a plug formed in the genital tract of the female, the length of which varied from 2.1 to 3.8 (*n* = 7; 3.0 ± 0.34) mm and the width was 1.1–2.1 (1.5 ± 0.20) mm. The plugs are removed at the next series of copulation. Two species were characterized by the male falling on his side after ejaculation, but this was rarely observed in *T. daghestanicus* (Table 3).

Discussion

During the Pleistocene glacial period, the Lankaran region of Azerbaijan was protected from the invasion of cold air masses by the Talysh mountain system and the sea, and became a refugium for many thermophilic plant species, forming a unique biotope (Akhani *et al*., 2010). Apparently, isolation determined the specific

Table 3. Comparison of copulatory parameters of *M. schelkovnikovi*, *M. obscurus* and *Terricola daghestanicus*. Statistical information is presented as follows: n — a number of observations; arithmetic mean ± standard error.

Parameters	*Microtus obscurus* *n* = 10	*M. schelkovnikovi.* *n* =15	*T. daghestanicus* *n* = 10
EF	4.4 ± 0.30	2.47 ± 0.17	3.8 ± 0.20
Σ IF	46.8 ± 4.50	23.1 ± 2.31	24.8 ± 5.82
Σ NT	71.6 ± 6.61	45.3 ± 4.76	63.6 ± 5.27
IF 1st series	9.8 ± 1.02	7.5 ± 0.53	8.8 ± 1.18
T/I 1st series	1.6 ± 0.13	2.0 ± 0.19	2.6 ± 0.31
T/E 1st series	1.0	1.1 ± 0.09	1.4 ± 0.40
NT 1st series	14.8 ± 1.61	16.4 ± 1.25	22.4 ± 2.46
DC, s	108.7 ± 9.77	92.7 ± 9.85	120.0 ± 26.32
PEI, s	290.0 ± 25.85	737.0 ± 58.2	229.0 ± 21.06
L, s	568.2 ± 92.83	902.7 ± 159.7	917.0 ± 203.0
% of ejaculations with one thrust	95.5	86.5	83.3
Proportion of males falling on his side after ejaculation, %	56.5	53.0	10.0

adaptation of Shelkovnikov's vole to the habitats of Talysh, as well as the features of its morphology and biology. In different habitats bordering the Hyrcanian forest, other species of voles were caught as well, for example, the social vole *M. socialis* lived in the steppes, and the common vole *M. obscurus* was found in meadows at an altitude of 1400 m above sea level. According to our observations, Schelkovnikov's vole is not characterized by an underground lifestyle. Voles prefer to use ready-made burrows or make surface passages under a layer of foliage at a depth of no more than 5 cm; the tunnels can reach several meters in length. This may be due to the characteristics of the soil, which becomes compacted during dry periods and gets wet during rainy periods (for example, clay layers). Nests are arranged along the roots of trees at a depth of 20–40 cm (Kadatsky, 1964; Steiner, 1972; Khatukhov & Tembotov, 1982; personal observation).

In the study area, clearly audible vocalizations such as squeaks were repeatedly recorded, which indicates social interactions between animals. These observations are confirmed by open-field test data (Zorenko *et al.,* 1989). Individuals of this species are active; quickly begin to explore a new space without showing noticeable fear (signs of which include immobility, delay in first crossing the test field and defecation). Thus, *M. schelkovnikovi* immobility (median) is 100 s, field crossing was 188 s and the rate of defecation was 0 per 10-minute experiment, while in *T. daghestanicus* it was 168 s, 600 and 4, respectively. The specific behaviour of the two species in the open field test correlates with their adaptation to different habitats. The first species lives in open, poorly lit forest under the crowns of trees and moves along the surface, while the second species lives in meadows and moves along paths under grass cover.

There is no data on the diet of the species, but it is believed that *M. schelkovnikovi* feed on underground parts (rootstock, tubers) of plants and seeds (Kadatsky, 1964; Steiner, 1972). Possibly, the majority of the vole's diet consists of leaves, fruits, seeds and roots of trees and shrubs. Trees such as alder, maple and Persian ironwood have small roots ranging from 0.29 to 4.70 mm in diameter, which are in the upper soil layer at a depth of about 10 cm (Abdi & Deljouei, 2019). They may be edible. In current study, voles were fed a standard diet commonly used under laboratory conditions. Possibly, this food did not fully satisfy the physiological needs of *M. schelkovnikovi*, which led to increased mortality of the pups.

Estimates of the species' abundance are contradictory. Vereshchagin (1949) considered *M. schelkovnikovi* a rare species, while Khatukhov and Tembotov (1982) considered it common in suitable habitats. The average number of voles is 5.1% per 100 trap-days, the maximum is 12.0%.

These authors indicate that in May 1977, 62 individuals were caught in 20 live traps in 1.5 days. In Iran, the number of voles was lower, on average 0.43–3.03% per 100 trap-days (Steiner, 1972). My captures in the first half of June 1988 showed an abundance of 3.3%. Apparently, Schelkovnikov's vole may be a common species in suitable habitats, but additional research is needed to clarify the population dynamics.

There are no field breeding data; however, laboratory studies indicate that *M. schelkovnikovi* has a lower pregnancy rate, small litter size, and longer reproductive life cycle than many other vole species (Meyer *et al*., 1996; Zorenko, 2013). The laboratory data show seasonality of reproduction, which can be noted in natural habitats as well. The winter and summer pause in reproduction is associated with changes in temperature and humidity. Both dry and hot periods (average temperature in July and August was 28°C) and cold and snowy periods (in January it was 2.5–3.0°C) can affect vegetation and reduce the ability of reproduction.

The social behaviour of Schelkovnikov's vole is not qualitatively different from the behaviour of most studied vole species (Colvin, 1973; Zorenko, 1994, 2013). In general, *M. schelkovnikovi* males are characterized by contact avoidance and ritualized aggression towards individuals of the same sex. At the same time, males show great interest in females and initiate friendly contacts. The results show that vocalization is one of the predominant behavioural patterns in same-sex and opposite-sex animals. Although the vocalization in voles is mainly associated with their emotional state (Rutovskaya, 2019) the functional role of such behaviour cannot be excluded. Vocalization probably contributes to the avoidance of contacts and serves as the manifestation of direct aggression between males, as well as synchronizes the behaviour of females and males during mating.

The development of Shelkovnikov's vole in early postnatal ontogenesis is similar to most species of voles of the tribe Arvicolini (Zorenko, 1981; Zimová, 1987; Zorenko *et al*., 1994; Meyer *et al*., 1996). However, the development of morphological characteristics of *M. schelkovnikovi* pups occurs more slowly; their formation is fully completed only by the 15th day. On the contrary, in the species of voles *Microtus* s. str. formation of exterior signs is fully completed by the 11th day (Zorenko, 1981), *Sumeriomys* — by the 11th–13th day (Zorenko, 2013), *T. daghestanicus* — by the 11th day (Mambetov, 1987) and *T. subterraneus* Sélys, 1836 — by 14th day (Zimová, 1985).

The results allow us to reconstruct the social structure of the species. The Schelkovnikov's vole, apparently, can be considered a monogamous species. This is indicated by both direct observations of *M. schelkovnikovi*, and by several indirect indicators. An indirect sign may be an equal ratio of breeding males and females during capture in the summer of 1988, which promotes the formation of monogamous pairs. Kohiya (1952) showed that *M. socialis goriensis* successfully reproduces with a sex ratio of 1:1, as voles can form pairs. Mating in *M. schelkovnikovi* occurs only between familiar voles from the formed pair. This is confirmed by other features identified when analysing the behaviour of *M. schelkovnikovi*. This species is characterized by a small number of ejaculations (2.47), which is consistent with the assumption of an inverse relationship between EF and reproductive strategy (Dewsbury, 1981).

Thus, typically monogamous *Mynomes ochrogaster* Wagner, 1842 (Gray & Dewsbury, 1973) and *M. socialis* (Zorenko, 2000) had 2.2 and 2.7 ejaculations, respectively. Species such as *Mynomes californicus* Peale, 1848 (Kenney *et al*., 1979) and *Lasiopodomys mandarinus* Milne-Edwards, 1871 (Zorenko *et al*., 1994) also recorded a low number of ejaculations (2.2), although they exhibited not only social monogamy, but also polygyny (Smorkacheva & Orlova, 2011). Low play activity and late sexual maturation of Shelkovnikov's vole (Zorenko & Anderson, 1996) are another characteristic of monogamous species. However, late puberty may be associated with reproduction pauses in summer and winter.

The small index of relative testes size proposed by Heske & Ostfeld (1990) together with the low mass of male testes and vesicular glands may also be the sign of social monogamy. For comparison, the length of the testes in *T. daghestanicus* and *M. schelkovnikovi* is similar, while the mass of the testes differs significantly: in the first species it is 350–700 mg (Mambetov, 1987), depending on the breeding month, and in the second it is 63–94 mg. The index of the relative size of the testes in *M. schelkovnikovi* was 0.059 and in *T. daghestanicus* — 0.07. However, in *M. socialis* with social monogamy proved in nature (Kasatkin *et al*., 1998; Shilova & Kasatkin, 2000) and in laboratory (Zorenko, 2013), the mass of the testes is 377 mg, and the index of the relative size of the testes is 0.10, which corresponds more to a promiscuous breeding strategy rather than monogamy. Some data suggests that testes mass tends to be lower in species with small litter size and induced ovulation (Soulsbury, 2010). However, ovulation is induced in most or all voles (Breed, 1967; Jemiolo, 1983; Zorenko, 2013). Thus, the data on the correlation of these indicators in voles are contradictory and require additional studies.

Copulatory behaviour is based primarily on instinctive components; it is conservative and very stereotyped. It can be assumed that the copulation stereotype has a noticeable phylogenetic signal. The copulatory stereotype of *M. schelkovnikovi* is characterized by a small number of ejaculations, triggered by many intromissions and an average level of genital stimulation. Although Schelkovnikov's vole is a species of an independent subgenus *Hyrcanicola* within the genus *Microtus* (Nadachowski, 2007), its copulatory stereotype does not differ significantly from the behaviour in species of the subgenus *Microtus* s. str. (Zorenko & Malygin, 1984; Zorenko & Zakharov, 1987) and the subgenus *Sumeriomys* (Zorenko, 2000), as well as from *Terricola daghestanicus*. Almost all differences are quantitative, while the basic type of copulatory stereotype is similar. The species of the genera *Microtus* (with the subgenera *Microtus* s. str. and *Sumeriomys* Argyropulo, 1933) and *Terricola* Fatio, 1867 have a similar principle of implementation of the copulatory stereotype. In all species of the listed taxa, the copulatory stereotype has common features: a large number of intromissions, a small number of ejaculations and an average level of genital stimulation.

These taxa are included in the Palearctic branch of voles; its formation took place in the Western Palearctic (Abramson *et al*., 2021). Molecular studies show that the divergence between these lineages corresponds to the late Pliocene; however, speciation events coincided with the Early Pleistocene for the genus *Terricola* (separated from the genus *Microtus* 1.38 Mya) and the Early Middle Pleistocene for the subgenera *Sumeriomys* and *Microtus* (Abramson *et al*., 2021). Therefore, it can be assumed that a similar principle of copulatory stereotype organization is not the result of parallelism but stems from the common origin of taxa.

The described copulatory stereotype is fundamentally different from another stereotype recorded in the Asian branch, represented by the genera *Alexandromys*, *Lasiopodomys* (Zorenko, 2007; Zorenko & Atanasov, 2017, 2018) and *Neodon* (unpublished data). It is characterized by the absence or small number of intromissions, many of ejaculations and a high level of genital stimulation. Interestingly, such a peculiar behavioural pattern as the male falling on his side after ejaculation is widely represented in all species of the Western Palearctic lineage and is rare in the Asian lineage. The fewer thrusts the ejaculatory mount includes, the more likely it is that the male will perform falling. The connection between these mating patterns is confirmed by the Spearman rank correlation coefficient of 0.909 (calculated for 16 species of voles). The level of genital stimulation is an important parameter, which is necessary, on the one hand, to activate the ejaculatory mechanism, and on the other hand, to induce ovulation in the female (Dewsbury, 1975). During the courtship, males can sing, but singing is manifested with different probability in different taxa. In the Western Palearctic branch (species of *Sumeriomys*, *Microtus* s. str. and *Terricola*) the percentage of singing males is small (from 5 to 25). In the Asian Palearctic branch (species *Alexandromys* and *Lasiopodomys*), singing was observed in the majority of males (from 50 to 100% depending on the species).

Conclusion: it is important to continue studying the ecology of this species, unique in its range. However, the intensification of human activity in this threatened forest zone has made conservation a top priority (Ghorbanalizadeh & Akhani, 2021). Accordingly, in 2019, the Hyrcanian Forests were inscribed as a UNESCO World Heritage property. *M. schelkovnikovi* is listed on the IUCN Red List of Threatened Species (Kennerley, 2016).

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