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Make haste slowly: reproduction in the Zaisan mole-vole, *Ellobius tancrei*

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Mole-voles are the most specialized subterranean members of the subfamily Arvicolinae. We assess the basic reproductive parameters of the Zaisan mole-vole and compare our data with the characteristics reported for other *Ellobius* species and surface-dwelling voles. In most respects reproduction of the *E. tancrei* (Blasius, 1884) follows the pattern that is typical for voles. Females undergo postpartum estrus, but rarely combine pregnancy with lactation. The rate of embryonic and postembryonic growth (respectively, 0.13 and 0.54 g/day) are slightly lower, while the relative neonate and weanling masses (respectively, 8% and 40% of maternal mass) are slightly higher than the respective values predicted for non-subterranean arvicolines. The combination of these trends results in the protracted pregnancy and lactation (both ~30 days). The age at first breeding is delayed (>2.5 months). Despite heavy weanlings, total maternal investment per litter in *E. tancrei* is low due to small litter size (2.31). While the species of *Ellobius* are similar to each other by the parameters of developmental time, they vary by litter size, total investment per litter, and possibly by relative neonate body mass. This is consistent with the idea that when body size effect is removed, fecundity variables and degree of precociality at birth are dissociated from timing variables.

Key words: Zaisan mole-vole, *Ellobius tancrei*, subterranean rodents, slow life-history, reproduction, growth, sexual maturation

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Introduction

One of the primary goals of life history studies is revealing ecological, physiological, and phylogenetic factors which influence how organisms allocate energy to reproduction. The comparative investigations of the last decades led to the concept of a mass-independent “fast-slow continuum” which implies that life-history traits co-vary systematically when body size effects are removed. At the “fast end” are species that, for their body size, mature quickly, give birth frequently, and wean large litters of small offspring early, while species at the other end have the opposite suite of traits. The differences between taxa in speed of life-history are shaped by the variations in mortality rates and limitations in food supply imposed by different lifestyles, and are constrained by phylogenetic influence (Stearns 1983; Gaillard et al. 1989; Read and Harvey 1989; Bielby et al. 2007; Sibly and Brown 2007; Sibly et al. 2012).

For highly specialized subterranean animals slow life history can be undoubtedly predicted. First, living in safe and stable subterranean burrows should result in low extrinsic rates of mortality and therefore in the selection for the slow life history (Nevo 1979; 1999; Burda 2007; Sibly and Brown 2007). Second, most subterranean rodents have reduced basal metabolic rate (McNab 1979; Buffenstein 2000). This physiological variable is thought to correlate positively with fecundity through its impact on mass-independent growth rate, time from conception to weaning, and other life-history parameters (Glazier 1985; Thompson 1992; McNab 2006, but see Read and Harvey 1989). In addition, Novikov suggested that high energetic costs of foraging by digging (Vleck 1979; Lovegrove 1989; Luna et al. 2002; Zelová et al. 2010) should be compensated for by low energetic costs of reproduction (Moshkin et al. 2007; Novikov 2007). Therefore, the subterranean rodents are expected to be characterized (for their sizes) by high longevity, late sexual maturation, prolonged gestation, slow postnatal development, low growth rate, long interbirth intervals and/or low reproductive efforts per litter, and as a result low productivity. These theoretical predictions are

generally supported by the available empirical data (Nevo 1979, 1999; Begall et al. 1999; Bennett et al. 2000, 2007; Šumbera et al. 2003; Damman and Burda 2007).

Traditionally, slower life-history has been associated with higher maternal investment per offspring and more precocious newborn (Pianka 1970; Stearns 1983). However, the results of several recent comparative analyses for mammals suggest that after adjustment for body mass and phylogeny these variables may not be correlated with the gradient contrasting species with short fast lives and ones with long slow lives (Bielby et al. 2007; Dobson and Oli 2007^{a,b}). Low energy allocation per litter supposed for subterranean rodents might be associated with decreased litter size, decreased offspring size, or both. Therefore, there is no clear prediction about the litter size, parental investment and degree of precociality associated with this lifestyle. Concerning the altriciality/precociality axis of life-history variation, the comparative data for Hystricognathi provide some evidences for the tendency for altriciality in subterranean species (Camin 2010). The respective data for other rodent taxa are lacking. Revealing the life-history correlates of living underground is impeded by the fact that most truly subterranean Sciurognath rodents have no closely related surface-dwelling taxa.

Genus *Ellobius*, mole-voles, represents a remarkable model for evolutionary ecologists. Mole-voles are the most specialized subterranean members of the subfamily Arvicolinae (Ognev 1948; Lacey et al. 2000). The Arvicolinae is one of the youngest rodent group, and the subterranean lifestyle evolved in *Ellobius* only recently (supposed time of separation from surface-dwelling voles around 3.3-5.8 Myr - Abramson et. al. 2009). Moreover, the Arvicolinae is known as a group located at the extreme of fast end of the fast-slow continuum. Thus, the comparison between mole-voles and surface-dwelling voles provides the unique opportunity to reveal those shifts in life history parameters which arise at the beginning of the evolutionary track to underground.

At present, the information on the life history characteristics for all species of mole-voles is scarce. In accordance with the expected for a subterranean rodent pattern, *Ellobius talpinus* (Pallas, 1770) has extreme longevity (about six years both in field and in laboratory), in comparison with

other vole species (Evdokimov 2001; Novikov 2007; Novikov et al. 2015). Some authors provide embryo counts and lengths of breeding season (*Ellobius tancrei* Blasius, 1884 - Meklenburtsev 1937; Rakov 1954; Slastenina 1963; Davydov 1988; *E. talpinus* - Zubko and Ostryakov 1961; Evdokimov 2001; *Ellobius lutescens* Thomas 1897; Coşkun and Uluturk 2003). There exist considerable discrepancies among different researchers in the estimates of pregnancy duration (21 to 30 days) and age of maturity (3 months to 1 year) (Meklenburtsev 1937; Shubin 1961; Zubko and Ostryakov 1961; Evdokimov 2001; Kaya and Coşkun 2015). The descriptions of the mole-vole postnatal ontogeny (*E. talpinus* - Letitskaya 1984; *E. lutescens* - Kaya and Coşkun 2015) support very slow development of young. In all published papers the information on offspring body mass, growth rate, and age of weaning is based on very small sample sizes. Novikov (2007) compared litter size, neonate and weanling masses and inter-litter interval in red-backed voles (genus *Myodes*), dwarf hamster (*Phodopus sungorus* Pallas, 1773), and northern mole-vole (*E. talpinus*), and concluded that the last species has relatively low reproductive effort. This proposition should be verified by a multi-species analysis accounting for body size and phylogeny.

In this study we assess the basic reproductive parameters for the Zaisan mole-vole. We then use these data and the available information for other arvicolines, including two *Ellobius* species, to test whether mole-voles have longer gestation and lactation periods, lower growth rate, delayed sexual maturation and lower investment per litter, in comparison with other voles. We also test if the maternal investment per offspring and developmental state of newborn in *Ellobius* differs from that in other voles.

Material and methods

Reproductive data for E. tancrei

Animals and housing

The Zaisan mole-voles used in this study are the descendants of eight animals (six males and two females) originating from South-West Tajikistan. In this region, *E. tancrei* displays variety in chromosome numbers (2n from 30 to 53) (Bakloushinskaya et al. 2013). Our animals belong to the

form with $2n=33/34$. This study is based on the data obtained for animals of second-sixth laboratory generations.

Mole-voles were housed in glass terraria (25 cm × 50 cm × 30 cm) half-filled with wood shavings. Toilet paper served as nest material. Carrots, apples, beets, pumpkins, oats, bran, and willow twigs were provided ad lib; mashed meat was given in small amount twice a week. All animals were housed under a 16/8-h light/dark cycle at an ambient temperature of 19–22°C. Mole-voles were kept as family groups consisting of a breeding male, a breeding female and offspring from one-two litters, the group composition reported for free-living *E. tancrei* (Meklenburtsev 1937; Davydov 1988). In most cases offspring were separated from their natal group at the age of about 4-6 months and after some period of isolation (1-6 weeks) were paired with an unfamiliar mole-vole of the opposite sex. Given the small number of founders, we paid attention to preventing close inbreeding using information on pedigree. The widowed animals received new partners. Animals receiving new mates were considered sexual experienced.

Obtaining data

The most reliable way to determine exact pregnancy duration would to remove a male from the female's cage just after the copulation has been recorded, and to determine the elapsed time until the birth of the litter. However, our observations showed that only a small proportion of all copulations results in successful pregnancies. In addition, in some monogamous species removal of a male can result in pregnancy failure (Norris 1985; Roberts et al. 1998). Thus, we did not separated members of a pair. Instead, we determined a minimum interval from occurrence of spermatozoa in vaginal smears up to delivery. We monitored 16 females from pairing until the birth of the litter or for 90 days. We examined the females daily during the first week after pairing and twice a week thereafter for vaginal perforation. Vaginal smears were taken when wide vaginal opening was detected.

To test the occurrence of the postpartum estrus, we took vaginal smears from eleven females within 24 h after delivery. In *Ellobius*, cytological constitution of a vaginal smear is not a reliable

indicator of female receptivity, so we used the presence of spermatozoa in smears as the evidence of the postpartum mating.

The intervals from the pairing to the birth of the first litter, inter-birth intervals and litter sizes were determined for 36 successfully breeding pairs of mole-voles. Twelve pairs were formed of inexperienced mates, seven pairs consisted of experienced mates, ten pairs included inexperienced female and experienced male, and seven pairs included experienced female and inexperienced male. All these animals were older than five months at pairing. After pairing, they were left undisturbed except weekly weighting (to the nearest 0.1 g) and inspecting females for nipple prominence and vaginal perforation. Cages with pregnant females were checked daily for litters. We determined 36 intervals from pairing up to the first litter and 93 inter-birth intervals. In total, 144 litters were obtained. Litter size at birth (=within 24 h of parturition, day 0) was determined for 51 litters while the manipulations with the remaining 93 litters have been started at day 1-2 after parturition to prevent the disturbance of new mothers. The annual reproductive output (the number of litters and the number of delivered offspring) was calculated for 13 females continuously housed with a male for at least 12 months.

We determined body mass to the nearest of 0.1 g at birth (= within 24 hours after delivery) for 118 pups from 51 litters. Mean growth rate as well as body mass at weaning (28-30 days, see Results) were determined for 90 pups (43 males and 47 females) from 46 litters based on weekly weighting. We weekly registered the nipple condition (discharge milk or not) of the dams which had offspring younger than two months. The occasional observations of suckling and feeding solid food by juveniles between 25 and 45 days were recorded.

Within the span of this study, 52 young females born to 36 dams were kept with their natal group until at least six months. Thirty six of these females were examined at least twice a week for the vaginal opening until the age of 90 days. All young females were weekly examined for the signs of pregnancy while staying with their parents. Eight young females and five young males were caged with an opposite sex, unrelated sexually experienced animals at 50-90 days of age to

determine the earliest age at which young male and female can copulate and the age at which they are fertile. From our previous experience, juvenile mole-voles may be separated from their parents at 45 to 55 days when their body mass is of about 32-33 g. The earliest age and weight at sexual maturation suggested in literature is about 3 months and 30-36 g, respectively (Shubin 1961; Zubko and Ostryakov 1961). These time limits determined the ages when the young individuals were mated. The females were checked for vaginal perforation, and vaginal smears were taken daily for a week after pairing.

Statistical analysis

We compared the intervals up to the next birth in cases when at least one offspring was successfully weaned with that in cases when all pups died by day 15 (approximately the middle of lactation, see Results) using non-parametric Mann-Whitney test. A few instances of pup mortality at late lactation were excluded from this analysis).

We used the data for the first-fourth litters ($n=90$) to test the effects of litter order (four levels) and the point of measuring the litter size (two levels: at birth or at days 1-2 after delivery) on the litter size with two-way ANOVA. We tested the effect of dam's age (in months) on litter size using linear regression. Twelve litters delivered by primiparous females (age from five to 18 months) and measured at birth were included into this analysis.

The relationship between litter size and neonate body mass was investigated with linear regression analysis using the averaged values for all littermates (n litters = 51). Sex difference in body mass at weaning was assessed with Student's t -test.

All tests were two-tailed. Statistical significance in all cases was $\alpha = 0.05$. Most values are presented as means with standard deviations.

Reproductive parameters of Ellobius in relation to surface-dwelling voles

Data set

Data on maternal mass, pregnancy duration, neonate mass, weaning age, weaning mass, litter size, unweaned offspring growth rate, and age at sexual maturity were obtained from literature

for 38 vole species, including two species of mole-voles (Table. S, Supplementary data). When possible, we obtained all parameters for a given species from the same work to make estimates of indexes (see below) more reliable. We did not include the data for *Ondatra* and *Neofiber* in our dataset because both species are highly aquatic, and their inclusion as a size outlier would result in a disproportionate effect in any regression on body mass.

Where direct measures of offspring postnatal growth rate were unavailable, this parameter was calculated by dividing the weaning mass by the lactation length. The mean embryonic growth rate was found for each species by dividing the neonate mass by the length of pregnancy. We calculated the relative neonate mass and relative weanling mass as mean offspring mass at birth and mean offspring mass at weaning, respectively, divided by mean maternal mass. These parameters were used as mass-specific indexes of the amount of maternal investment per offspring up to the time of parturition and up to weaning (Austin and Short 1984; Charnov and Ernest 2006; Dobson and Oli 2007a,b). Relative litter masses at weaning calculated as the product of mean litter size and mean weanling mass was used as proxy of the total maternal allocation per litter. We estimated allocation per litter based on neonate litter sizes rather than the actual number of individuals weaned. The calculation of the last parameter would require the information on juvenile mortality which is affected by housing conditions and is seldom reported.

Statistical analyses

We used the data obtained for *E. tancrei* and life-history information for other species to test if the mole-voles significantly differ from non-subterranean arvicolines by growth rates, relative mass of offspring and relative litter mass.

In mammals, maternal body mass is positively related to growth rate; it can also be related to proportional offspring mass and litter mass (Austin and Short 1984; Reiss 1985). To remove the possible confounding effects of maternal body mass the approach described by Cooper and Withers (2006) was applied. We first determined the allometric relationship between body mass and each of reproductive variables in question for surface-dwelling arvicolines. Then we found the predicted

values and 95% prediction limits (PI) for *E. tancrei* (our data), *E. talpinus* (based on Zubko and Ostryakov 1961, and Novikov 2007), and *E. lutescens* (based on Kaya and Coşkun 2015), given their body masses, and assessed, for each of these species, whether the actual values lie outside the 95% prediction limits.

Phylogeny may influence life-history characteristics. Unfortunately, despite an impressive insight into Arvicolinae phylogeny, phylogenetic relationships between many members of this subfamily whose reproductive characteristics are available (genera *Lemmus*, *Dicrostonyx*, *Lemmys*, *Phenacomys*, *Arborimus*, most American species of *Microtus*) remain to be established (Galewski 2007; Buzan et al. 2008; Abramson et al. 2009). This made applying of any phylogenetically informed statistical analysis impossible. To reduce the phylogenetic pseudo-replication at least to some extent, and to avoid bias of results by one species-rich genus, *Microtus* we performed the additional analyses with average generic values (Harvey et al. 1980). The generic values for *Ellobius* were calculated based on our data for *E. tancrei* and available information for *E. talpinus* and *E. lutescens*.

Results

Reproductive characteristics of E. tancrei

Minimum interval from pairing to the birth of the first litter was 33 days for the pairs including experienced females and 40 days for the pairs including inexperienced females. The minimum intervals from the occurrence of spermatozoa in vaginal smears until delivery in six females were 29, 30, 30, 30, 31, 31 days. We found spermatozoa in the vaginal smears taken from six females within 24 hours after parturition, while the smears taken from other five females did not show evidence of postpartum mating.

Litters were born all year around. The smallest interbirth interval was 31 days, but most intervals fall between 40 and 90 days (Fig.1). The intervals up to the next delivery was longer when pups had survived than when pups had died (Mann-Whitney test: $Z=3.14$; $N_1=73$; $N_2=18$; $p=0.002$;

Fig.1). Thirteen females, each continuously housed with a male for 12 months, produced 4.0 ± 1.0 litters (range=2-6) including 8.8 ± 2.0 pups (range=5-13).

The basic parameters which characterize the reproductive allocation in *E. tancrei* are presented in Table 1.

For the litters from first to fourth there were significant effects of both litter order (two-way ANOVA: $F=5.09$; $df=3, 82$; $p=0.003$) and the point of measuring the litter ($F=5.45$; $df=1, 82$; $p=0.022$) on the number of neonates; the interaction effect was insignificant ($F=0.90$; $df=3, 82$; $p=0.444$). Overall, litter size increased from the first (at birth: 2.25 ± 0.96 , $n=12$; at days 1-2: 1.76 ± 0.53 ; $n=20$) to the fourth litter (at birth: 3.17 ± 0.75 , $n=6$; at days 1-2: 2.5 ± 0.76 ; $n=8$). The linear regression revealed the significant positive effect of dam's age on the size of the first litter ($F=13.11$; $df=1, 10$; $p=0.005$; $r^2=0.52$).

Offspring body mass at birth significantly decreased with litter size ($F=9.84$; $df=1, 49$; $p=0.029$; $r^2=0.17$). Maternal nipples discharged milk until at least 26 days but usually longer (Table 1). Though juveniles ingested solid food after 25-27 days, suckling was occasionally observed until days 35-40. In case of dam's death on day 35 postpartum the juveniles remaining with the father and older sibs survived, their growth and development did not appear to be affected.

There was no significant difference in body mass at weaning between male and female offspring (respectively, 19.6 ± 2.53 and 19.6 ± 2.31 ; Student's t -test: $t=0.08$; $df=88$; $p=0.938$).

Of 36 young females monitored for vaginal opening until the age of 90 days, eleven individuals (31%) displayed perforated vaginas at least once by 40 days, twenty individuals (56%) – by 60 days, and 26 individuals (72%) – by 90 days. Mean female age at first record of vaginal perforation was 48.0 ± 14.6 (range 30-86; $n=26$). After first short perforation for one-three days most females became imperforate again, and it is possible that we missed vaginal opening of some females. Thus, the percentages we present are likely underestimated with respect to real proportions of individuals which underwent vaginal perforation, while mean age is to some extent overestimated.

Vast majority of the young females which stayed in the presence of both parents at least up to six months did not breed. However, one of 52 delivered at the age of 105 days which indicates the successful conception at about 75 days.

Of eight females paired at the precocious ages with adult strange males, four individuals displayed spermatozoa in smears within a week from pairing, indicating copulations at 60, 64, 75 and 90 days. A female paired at 74 days and inseminated at 75 days delivered at the age of five months, the remaining pairs did not reproduce.

The young male mated at the age of 70 days copulated on the third day after pairing and sired his first litter at 87 days. Other four males paired at ages of 60-85 days did not reproduce.

Comparison of growth rates, relative mass of offspring and relative litter mass in Ellobius and above-dwelling arvicolines

Embryonic growth rate is lower than predicted given the female body mass in each of three mole-vole species (Fig. 2a). The same is true for the average parameter for *Ellobius* (Fig. Sa). The relative neonate body mass is slightly higher than predicted in *E. tancrei* and *E. talpinus*, but lower than predicted in *E. lutescens* (Fig. 2b). The value of this variable averaged for three mole-vole species nearly equals the predicted value (Fig. Sb). Postembryonic growth rate is close to the predicted value in *E. talpinus* and lower than predicted in *E. tancrei* and *E. lutescens* (Fig. 2c). The average generic value slightly deviates from the predicted one in the same direction (Fig. Sc). Both the comparison based on the species and generic data showed that the relative mass of mole-vole weanling is higher than the value predicted for a vole of given body mass (Fig. 2d; Fig. Sd). The relative litter mass by weaning is lower than predicted in *E. tancrei* but higher than predicted in other two mole-vole species (Fig. 2e); the generic value of this parameter in *Ellobius* is only slightly higher than the predicted one (Fig. Se).

In most cases the observed values fall within the 95% PI, the only exception is the weaning body mass in *E. lutescens* (Fig. 2, Fig. S).

Discussion

Reproductive performance of E. tancrei and the comparison with other mole-vole species

Up to now exact duration of pregnancy in any *Ellobius* species was unknown; different authors have postulated gestation length of about 21 to 30 days (Table. S, Supplementary data), but provided no evidence. Our data are consistent with the gestation period of about 30 days. The slight difference between our value for *E. tancrei* and that reported by Zubko and Ostryakov (26-28 days) for *E. talpinus* may reflect the interspecies variation. According to Kaya and Coşkun (2015), the pregnancy duration of *E. lutescens* is 21 days, although the minimum interbirth intervals they recorded were 27-28 days. These authors do not explain how the length of gestation was determined. The duration of pregnancy in rodents, including voles, appears to be a rather conservative trait (Innes and Millar 1992; but see Burda 1989, and Bennett et al. 2000 for extraordinary intraspecies variations in this characteristic). Thus, the difference between closely related species by as much as 25-30%, if it is real, is very unusual and interesting phenomenon. We suppose, however, that additional evidences are desired.

This study is the first one where the occurrence of postpartum estrus in *Ellobius* is proved. Although *E. tancrei* post-parturient insemination occurs at least occasionally, most of inter-birth intervals are much longer than pregnancy duration. The delayed implantation during lactation does not explain this pattern, judging from the distribution of the intervals. The likelihood of the successful gestating by lactating females was greater if pups had died before the middle of lactation period. Thus, either the pups of the dams impregnated postpartum suffer from high early mortality, or lactating females tend to sacrifice the gestated litter. The last proposition is more plausible because, other things being equal, the mothers are expected to promote the survival of those offspring which are less costly. It is the strategy that has been reported for rats in the situation of food deprivation (Woodside et al. 1983). Whatever the mechanism, Zaisan mole-voles clearly tend to avoid the concurrence between lactation and gestation. Our data are consistent with interbirth intervals suggested for free-living *E. tancrei* (1.5-2 months - Meklenburtsev 1937) and *E. talpinus* (35 days to 2.5-3 months - Shubin 1961; Zubko and Ostryakov 1961).

Scanty published data show significant interspecies and intraspecies variation in *Ellobius* litter sizes with mean number of embryos ranging from 2.6 (*E. tancrei* from South-East Kazakhstan - Rakov 1954) to 6.1 (*E. talpinus* from Central Kazakhstan - Shubin 1961). Mean litter size registered in our laboratory colony is similar to that established in free-living mole-voles from Tajikistan (mean number of embryos = 3.1; mean number of pups in excavated nests = 2.4 - Davydov 1988). This value is small in comparison with that of mole-voles populations from other regions and most non-subterranean vole species (Table S, Supplementary data). The all-year breeding of *E. tancrei* in South-West Tajikistan (Davydov 1988; Saidov 2010) may allow female to increase the number of litters per year at the cost of litter size. Based on the interbirth intervals and individual reproductive output recorded in captivity, females can produce at least four litters per year, as it has been proposed by Meklenburtsev (1937).

We found a significant positive effect of maternal age on the size of the 1st litter, the pattern reported for several rodent species (Negus and Pinter 1965; Kennedy and Kennedy 1972; Havelka and Millar 2004, but see Tkadlec and Krejčová 2001). Our study was not specially designed to disentangle influences of age and parity. Testing relationship between age and litter size in multiparous females would be confounded by the effect of interbirth intervals. Thus, we are uncertain whether the revealed increase in litter size from 1st to subsequent litters was due to advancing age, previous reproductive performance, or a combination of age and parity.

In our laboratory only approximately 2/3 of juveniles survived up to weaning, and the similar level of pup mortality may be inferred from the data presented by Kaya and Coşkun (2015). Infanticide or the lack of maternal care seems to be the most probable causes of mortality. Though the high rate of juvenile deaths may be partly attributed to incompletely adequate conditions of captivity, there is evidence of high pup mortality (19 %) for a free-living population of *E. tancrei* (Davydov 1988).

Body weight at birth (3.95 g) of the Zaisan mole-vole in this study was heavier than all other measurements of neonatal mass reported for *Ellobius*. The discrepancy between our value and one

presented by Davydov for the same species is considerable (2.5 to 3.5 g), and we suppose that Davydov's data are based on the weights of largest embryos rather than newborns. The slightly smaller absolute and relative neonate masses reported for *E. talpinus* (respectively, about 3 g and 7.5% - Letitskaya 1984, Novikov 2007) may at least partly reflect the trade-off between number and size of offspring (Smith and Fretwell 1974). Relatively low (given the maternal mass) birth mass of *E. lutescens* is consistent with and therefore may be considered as an indirect evidence of shorter pregnancy duration.

Weaning is a gradual process. Taken together, dynamics of nipple condition in dam's, age at first eating solid food by juveniles, and minimum interbirth interval suggest lactation period in *E. tancrei* to last about 28-30 days. This value is intermediate between that reported for *E. talpinus* (25-26 days - Letitskaya 1984, Novikov 2007) and *E. lutescens* (30-35 days - Kaya and Coşkun 2015). It is worth to note that young Zaisan mole-voles are still dependent on the care provided by their parents for 3-4 weeks after weaning (Smorkatcheva and Kumaitova 2014). According to Davydov (1988) and Slastenina (1963), only the individuals heavier than 32-35 g, which mass is attained by approximately seven weeks in captive animals, enter traps. This observation indicates that extended parental care and delayed independency is not an artifact of captivity.

For any *Ellobius* species, information concerning the timing of maturation is speculative or based on sporadic observations (Shubin 1961; Zubko and Ostryakov 1961; Evdokimov 2001; Kaya and Coşkun 2015). By our data, males of *E. tancrei* are fertile by at least 3 months. Young females usually *became perforate* by 1.5-2 months and after being housed with a strange male could be *inseminated* at about two months. However, it is unlikely that female mole-vole can *conceive* at the age of less than 2.5 months, and even the pregnancy as early as this appears to be an extremely rare event, taking into account very infrequent occurrence of philopatric breeding, prolonged period up to independency and long period from pairing to the conception in virgin females.

Although the problem of social control of reproduction is beyond the framework of this article, the single case of inbred breeding of philopatric daughter needs some comments. The strong

incest-taboo does not seem to be characteristic of the Zaisan mole-vole. We observed several instances when one of older offspring became a breeder after the death of one of parents. So we suppose that social inhibition rather than mechanisms of incest-taboo may prevent the reproduction of young animals within natal groups. Accordingly, the above-mentioned exception may be associated with the disruption of the “normal” social hierarchy due to bad physical condition of an old female.

Comparison with non-subterranean voles

In accordance with the expectancy, pregnancy period is protracted at least in two of three mole-vole species as compared with majority of arvicolines (Table S, Supplementary data). All examined *Ellobius* species have very long lactation period and total developmental time. Aside from mole-voles, only three vole genera have the lengths of gestation longer than 24 days: muskrat, *Ondatra zibethicus* L., 1766 (25-27 days – Willner et al. 1980), round-tailed muskrat, *Neofiber alleni* True, 1884 (27 days – Birkenholz 1972) and tree voles of genus *Arborimus* (27 days as minimum in *Arborimus pomo* Johnson and George, 1991 – Hamilton 1962). Among them, *Ondatra* and *Neofiber* stand out because of their very large size as well as their aquatic lifestyle. In both tree voles and mole-voles, an exceptionally long developmental time is partly due to slightly lower than expected growth rate. In *A. pomo*, this trait has been explained by the energy-conversion constraints resulted from a fir needle diet (Hamilton 1962). Slow growth and development as well as low metabolism postulated for *E. talpinus* have been proposed to compensate for high energetic demands of subterranean foraging (Novikov 2007). In fact, the association between metabolic rate and growth rate in arvicolines needs to be reevaluated by a multi-species analysis taking body mass into account.

Reproductive effort can be separated into: (a) how frequently females reproduce, and (b) how much energy females invests in each of their litters. The tendency of female mole-vole to postpone the next pregnancy contrasts with continuous reproduction observed in most voles under laboratory conditions (Hasler 1975; Keller 1985). Among *Microtus*, inter-litter intervals

approximately equal to or slightly longer than the duration of pregnancy are typical for even several semi-subterranean species which, judging by low litter size and delayed sexual maturation, are selected for low reproductive rate (*Microtus pinetorum* Le Conte, 1830 – Solomon and Vandenberg 1994; *Microtus subterraneus* de Selys-Longchamps, 1836 – Jemioło 1983; *Microtus savii* de Selys-Longchamps, 1838 - Caroli et al. 2000). Thus, birth frequency under optimal conditions appears to be relatively conservative trait in arvicolines, yet mole-voles deviate in the direction expected for a slow-living organism.

The interspecies comparison of reproductive allocation per litter is impeded by intraspecies variations of litter size. Based on data available, there is no evidence for especially low reproductive investment per litter in mole-voles. While the relative litter mass by weaning is insignificantly lower than predicted in Tajic mole-voles producing small litters, these values are higher than the predicted in other *Ellobius* species. In female mole-vole rearing 4-6 juveniles (the litter size reported for several mole-vole populations) the relative investment per litter is high even by arvicoline standards. Subterranean dams rearing large litters should be hardly energetically compromised, and the presence of additional workers may be advantageous. The selection for greater female fecundity may explain the evolution of extreme philopatry and sociality described for northern populations of *Ellobius* (Evdokimov 2001).

Age at which voles become sexually mature depends on a number of factors (Nadeau 1985; Gower et al. 1992; Negus and Berger 1998; etc.). This intraspecies plasticity coupled with the lack of common procedures and measures used by various researchers complicates interspecies comparison; the reported values are usually rough or overestimated. Nevertheless, clear species differences are evident in the earliest age at which the successful conception is possible under optimal conditions (typically, when young animal is mated with an unfamiliar adult sexual partner). The available data strongly indicate the delay of fertility in mole-voles (>75 days for both sexes) in comparison with vast majority of arvicolines (15-47 days for females, 26-60 days for males - Table S, Supplementary data). Interestingly, *Ellobius* does not appear to be extreme in timing of another

sign of female puberty, first spontaneous (i.e. occurring in young individuals not exposed to male stimuli) vaginal perforation. Even overestimated, mean age at first vaginal opening in female mole-voles (48 days) is comparable to the values reported for several other vole species (26-43 days, Table S, Supplemented data). Thus, in female mole-voles, the age at earliest breeding is delayed in relation to the spontaneous onset of sexual maturation by several weeks, the pattern quite different from that of other examined voles.

The relatively large neonates in the Zaisan and northern mole-voles suggest that the tendency to deliver more altricial pups proposed for subterranean members of Hystricognath clade (Camin, 2010) does not meet in subterranean voles. Despite low postnatal growth rate, mole-vole weanlings are heavy due to extended lactation period. Keeping in mind the post-lactation period of parental care (Smorkatcheva and Kumaitova 2014), the total investment per offspring appears to be extremely high. Apparently, juvenile mole-voles have to acquire specific skills and foraging performance to handle the challenges posed by their subterranean lifestyle.

General conclusions

We realize that our analyses neglect possibly confounding effects of phylogenetic relationships among vole species and genera, and the results should be verified as the necessary phylogenetic information is available. Nonetheless, the validity of our main findings does not seem to depend on the phylogenetic correction. The dramatically slowing life history in *Ellobius* is achieved without significant modification in reproductive physiology through the appropriate combination of several trends: (i) protracting of (rather than decreasing) maternal investment per one reproductive episode, (ii) spreading out reproductive episodes by failing to gestate after parturition, and (iii) and delaying age at first breeding in relation to the onset of sexual maturation in females.

Three species of *Ellobius* are similar to each other by the prolonged developmental time, and clearly can be placed at the slow end of the “fast-slow” continuum. At least in voles, slow life-history is associated with larger investment per offspring. However, the mole-vole species

considerably differ by those parameters which characterize reproductive output per bout (litter size and total investment per litter). Unexpectedly, these species probably also differ from each other by the developmental stage at which young are born. This is consistent with the idea that when body size effect is removed, fecundity variables and degree of precociality at birth are dissociated from timing variables (Burda 1989a; Bielby et al. 2007; Dobson and Oli 2007a, b).

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Table 1. Characteristics of maternal investment in the Zaisan mole-vole, *Ellobius tancrei*

variable	<i>N</i>	Mean ± SD	lim
Litter size at birth	51	2.31 ± 0.86	1-4
Offspring body mass at birth, g (% of maternal mass)	118	3.95 ± 0.32 (8.10±0.85)	2.9-4.5 (6.3-10.2)
Growth rate, days 0-28 after birth (g/day)	90	0.54 ± 0.10	0.28-0.80
Offspring body mass at weaning, g (% of maternal mass)	90	19.6 ± 2.87 (40.3±5.45)	14.1-28.0 (22.9-56.2)
Last registration of milk discharge, days after delivery	42	33.2 ± 6.10	26-50

Figure legends

Fig.1. Distributions of interbirth intervals in female Zaisan mole-voles (*Ellobius tancrei*) in cases when at least one offspring was successfully weaned and when all pups died by the middle of lactation.

Fig.2. Offspring embryonic growth rate (a), relative body mass at birth (b), postembryonic growth rate (c), relative body mass at weaning (d), and relative litter mass by weaning (e) as a function of female body mass for arvicoline rodents. The values for three *Ellobius* species are depicted by closed circles. Dotted lines are 95% prediction intervals (values for *Ellobius* were not included in the prediction calculations).

Fig.S. Offspring embryonic growth rates (a), relative body mass at birth (b), postembryonic growth rate (c), relative body mass at weaning (d) and relative litter mass at weaning (e) as a function of female body mass for arvicolines rodents, based on average generic values. Red circles are for *Ellobius*, black circles are for other genera. Dotted lines are 95% prediction intervals (values for *Ellobius* were not included in the prediction calculations).

Fig.1. Distributions of interbirth intervals in female Zaisan mole-voles (*Ellobius tancrei*) in cases when at least one offspring was successfully weaned and when all pups died by the middle of lactation.

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