



Original investigation

Does sire replacement trigger plural reproduction in matrilineal groups of a singular breeder, *Ellobius tancrei*?



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ABSTRACT

Group-living species differ in how the reproduction is shared among same-sex individuals and how the reproductive skew is attained. In mammals, the highest level of reproductive skew among females is known for some social African mole-rats. Mole voles (*Ellobius*, Arvicolinae) are similar to these well-studied subterranean rodents in both ecological specialization and social structure. At present, there is no information about the proximate mechanisms underlying singular breeding in any *Ellobius* species. In this study of the Zaisan mole voles, *E. tancrei*, we tested the mother's influence on reproduction and survival of the young females exposed to an unrelated mate. Nine of 15 daughters housed in pairs bred, and all pairs persisted until the end of the experiment (6 months). The reproduction in the matrilineal trios (n = 12) was skewed towards mothers: only one daughter delivered but did not wean the litter. The latency until conception was significantly longer in paired daughters than in mothers from trios. Thus, the reproductive skew in trios may be initially generated by the age or experience difference rather than dominance asymmetry. Only 4 trios persisted for 6 months due to high female mortality. The heavier and older was a mother, and the younger was a daughter at male introduction, the more stable was the trio. The influence of females' ages on group tenacity may be mediated by the daughter's age-related reproductive activation. The despotic reproductive monopoly with extreme intolerance between kin reproductive females is unusual for voles and indicates a strong female–female competition in *E. tancrei* in nature.

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Introduction

Reproductive skew may be depicted as a continuum from the despotic pattern in which one female (or male) completely monopolizes reproduction to the egalitarian pattern in which all adult same-sex individuals produce offspring (Vehrencamp, 1983; Keller and Reeve, 1994). Closely related species or even populations of the same species may differ markedly in this respect. The reproductive skew in animal groups may be generated by a number of factors (Solomon and French, 1997; Reeve and Keller, 2001; Hager and Jones, 2009 and references therein). The lack of reproduction in a subset of individuals may be primary due to the disruption of their breeding attempts by breeders by means of behavioral or physiological suppression, eviction or infanticide. Alternatively or additionally, asymmetry between dominants and subordinates in age, condition, experience and access to unrelated breeding part-

ners may promote reproductive asymmetry even in the absence of social inhibition. Although several proximate mechanisms act in tandem to maintain a high reproductive skew in most of the studied cooperative species, there are obvious interspecies differences in the extent to which each contributes (French, 1997; Saltzman et al., 2004; Solomon et al., 2006; Faulkes and Bennett, 2009; Young, 2009). For example, in some predominantly singular breeders, the replacement of a sire by a new male results in the reproduction of several females, suggesting the subordinate's breeding to be mainly restricted by inbreeding avoidance (prairie vole, *Microtus ochrogaster* – Lyons and Getz, 1993; Wolff et al., 2001; pine vole, *Microtus pinetorum* – Brant et al., 1998; Mongolian gerbil, *Meriones unguiculatus* – Clarke and Galef, 2001; golden lion tamarin, *Leontopithecus rosalia* – French, 1997; Ansell's mole-rat, *Fukomys anselli* – Burda, 1995). On the other hand, in a number of species more or less close inbreeding is tolerated, unrelated immigrants are readily accepted to the breeding group, or mating outside the group is possible, yet the reproduction is highly skewed to only one female (naked mole-rat, *Heterocephalus glaber* – Lacey and Sherman, 1991; Alpine marmot, *Marmota marmota* – Hackländer et al., 2003; Damaraland mole-rat, *Fukomys damarensis* – Burland et al., 2004; meerkat, *Suri-*

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cata suricatta – Clutton-Brock et al., 1999; Griffin et al., 2003; dwarf mongoose, *Helogale parvula* – Creel et al., 1992). Interestingly, the degree of social inhibition varies not only among species but also among reproductive groups within a species or a population; it has been shown to depend on the quality of the pre-existing relationship between mother and daughter (common marmoset, *Callithrix jacchus* – Saltzman et al., 2004) or on the age asymmetry between females (*M. pinetorum* – Solomon et al., 2006). The information on the level and the proximate causes of breeding asymmetry in different species is critically important for the reproductive skew theory. First, such information provides knowledge of which reproductive skew models are applicable and therefore of which theoretical predictions may be tested. Second, comparative data allow testing the predicted links at the intra- or inter-species level (Johnstone and Cant, 2009; Hodge, 2009; Koenig et al., 2009; Saltzman et al., 2009; Young, 2009).

Mole voles (genus *Ellobius*, Arvicolinae) are highly specialized subterranean rodents that are widespread in the grasslands of Eurasia. Social organization has been reported for three of five recognized species: Zaisan mole vole, *E. tancrei* (Meklenburtsev, 1937; Slastenina, 1963; Shubin, 1978a; Davydov, 1988), Northern mole vole, *E. talpinus* (Evdokimov, 2001; Novikov et al., 2007) and Transcaucasian mole vole, *E. lutescens* (Coşkun and Uluturk, 2003). All these species live in family groups. Offspring are weaned at four-five weeks but becomes independent from parental care as late as about two months. Females may reach sexual maturity by 3–5 months and deliver up to 2–4 litters per year (Shubin, 1978a; Letitskaya, 1984; Davydov, 1988; Smorkatcheva and Kumaitova, 2014; Kaya and Coşkun, 2015; Smorkatcheva et al., 2016). Even in nature mole voles can survive for 6 years (Evdokimov, 2001; Novikov et al., 2015, 2017). In *E. talpinus* offspring stay in their natal burrow for several months to several years after weaning (Evdokimov, 2001). Dispersal age in *E. tancrei* is virtually unknown. Davydov (1988) suggested that young *E. tancrei* leave natal burrows at about 2–2.5 months. However, groups of the Zaisan mole voles may occasionally comprise up to 12–20 individuals, including offspring of three generations (Meklenburtsev, 1937; Slastenina, 1963; Davydov, 1988). Along with a small litter size, very slow post-natal development and large interbirth intervals, this suggests that dispersal may be at least occasionally delayed much longer. In captivity, the relationships among members of the extended families including parents and mature offspring are affiliate.

According to most authors, mole voles live in monogamous or polyandrous groups (*E. tancrei* – Slastenina, 1963; Shubin, 1978a; Davydov, 1988; *E. talpinus* – Evdokimov, 2001; *E. lutescens* – Coşkun and Uluturk, 2003), although polygyny is not uncommon in at least one population of *E. talpinus* (Novikov et al., 2007), and there is anecdotal evidence of plural reproduction in *E. tancrei* (Davydov, 1988). The low proportion of reproductive females (25–45%) noticed by many researchers is consistent with a high reproductive skew among females (Shubin, 1978a; Davydov, 1988; Evdokimov, 2001; Novikov et al., 2007). In our captive colony of *E. tancrei* the daughters housed with their natal families for up to nine months virtually never bred (Smorkatcheva et al., 2016).

Ellobius represents an especially interesting model for behavioral ecologists studying breeding systems and reproductive skew. On the one hand, the comparison between mole voles and closely related surface-dwelling voles provides the opportunity to reveal the fine-scale divergences in breeding systems and underlying mechanisms, and test their dependence on ecological and demographic factors (Crespi, 2009; Koenig et al., 2009; Taborsky, 2009). On the other hand, the social organization of the singular breeding mole vole species is strikingly similar to that of social bathyergids, which also live underground and display the highest level of reproductive skew known for mammals (Bennett et al., 2007; Faulkes and Bennett, 2009). The comparison between *Ellobius* and unre-

lated but ecologically and socially similar African mole-rats (family Bathyergidae) may yield insight into the relative importance of phylogeny and subterranean lifestyle in the evolution of reproductive skew. Meanwhile, there is no information about the proximate mechanisms which maintain skew among females in any species of mole voles.

The objective of this study was to evaluate the level of reproductive skew in the Zaisan mole vole matrilineal groups in which both a mother and a daughter have access to an unrelated mate, i. e. when the factor of incest avoidance is eliminated. Should a reproductive skew be present, our goal is to reveal whether it is underlain by the negative influence of a dominant, by some dominance-unrelated differences between two females (age or experience), or both of these factors.

Material and methods

The study was conducted at Saint Petersburg State University. Zaisan mole voles used in the experiment were the descendants of eight unrelated (trapped from the distant burrows) animals originating from southwestern Tajikistan. Given the small number of founders, we paid attention to prevent close inbreeding, using information on pedigree. This study is based on the data obtained for animals of second–sixth laboratory generations. Animals in our breeding colony typically were kept as family groups consisting of a breeding pair and offspring of one-two litters (see Smorkatcheva et al., 2016 for details of pair formation strategies). Mole voles were housed in glass terraria of different dimensions depending on the group size (25 cm X 50 cm X 30 cm for groups of 2–3 animals, 35 cm X 70 cm X 50 cm – for groups of 4–7 animals). Wood shavings and toilet paper served as bedding and nest material, respectively. Carrots, apples, beets, pumpkins, oats, and willow twigs were provided *ad libitum*; fresh salad and mashed meat were given weekly in small amounts. The animal room was maintained on a 16 h light: 8 h dark photoperiod at a temperature of 19–22 °C.

When focal young females were at the age of about 1.5 month, they were randomly assigned to one of two treatments. Females of the first treatment (D daughters) were removed from their natal families at 108–200 days of age and housed singly or with 1–2 littermates for 21–60 days. Young females of the second treatment (MD daughters) were separated, together with their mother, from the remaining members of a natal family at 114–194 days of age and housed as mother-daughter pairs for 18–109 days. Afterward, an unrelated unfamiliar male was introduced to the females' home cages. Ages of the young females at pairing ranged from 129 to 218 days (184 ± 27 ; here and thereafter the data are presented as $X \pm SD$) for D treatment and from 132 to 269 (183 ± 43) days for MD treatment. The mothers in MD treatment ranged in age from 360 to 1179 (722 ± 239) days. There were no significant differences among female categories in body mass at pairing (D daughters: 44.6 ± 4.90 g; MD daughters: 47.5 ± 6.22 g; MD mothers: 46.6 ± 3.47 g). Males ranged in age from 120 to 272 (188 ± 45) days and from 130 to 360 (221 ± 72) days in D and MD treatments, respectively (male Zaisan mole voles are fertile at about three months and are still reproductively active at five years of age – Smorkatcheva et al., 2016). All males excluding the oldest one in each treatment were sexually inexperienced and were kept alone or with 1–2 litter-mates for at least 1 week prior to being introduced to the focal females. The variation in the exact age of the animals was due to the limited number of available mole voles along with the unpredictable inter-birth intervals (Smorkatcheva et al., 2016). For the same reasons we ran the experiment in three sets. During each set, we monitored concurrently 3–5 groups of each treatment, providing total sample sizes of 15 and 12 for D and MD treatments,

respectively. All individuals but two females were used only once; two females were used first as D daughters and then as MD mothers.

Females were checked for vaginal condition just before the introduction of the male, and daily for the next week, and vaginal smears were taken when it was possible. The smears were air-dried, stained with the May Grunwald solution and analyzed later with a light microscope at magnification 280X. All groups were monitored for 6 months since the day of male introduction, or until the death of any group member. The duration of the experiment was set taking into account the prolonged period from pair formation until birth of the first litter in sexually inexperienced Zaisan mole voles (about three months on the average). With a six-month period, we provided the focal young females with extra time to realize their breeding potential. Through this period, all animals were weekly weighed and females were checked for signs of pregnancy. The cages were inspected at least every second day to record days of birth, injuries and deaths. Necropsies were conducted on dead voles to examine their reproductive condition at the time of death.

In females of a number of muroid rodents including voles, male-related stimuli induce rapid neuroendocrine changes leading to vaginal and behavioural estrus (Hasler, 1975; Milligan, 1980; Sawrey and Dewsbury, 1985; Seabloom, 1985). In voles, the reported latency from being paired with a male until estrus and copulation varied from 0 to 8 days, depending on species and female age (Jemiolo, 1983; Sawrey and Dewsbury, 1985; Smorkatcheva, 2002). At the beginning of this study, we expected to examine and compare the process of reproductive activation in females of three categories (D daughters, MD daughters and MD mothers) using vaginal smear dynamics and monitoring of sexual behavior. However, both of these approaches failed. The typical fluctuation of vaginal smear patterns was absent (see Results), and copulations could not be reliably registered as they occurred mostly in the nest and often were cryptic. Therefore, we had to confine ourselves to the comparison of the following reproductive variables:

- (i) proportions of females perforated on the day of male introduction (=day 0);
- (ii) proportions of females that were perforated by day 7 after male introduction (including only the individuals imperforated on day 0 and survived to day 7);
- (iii) latency until vaginal perforation (including only the individuals imperforated on day 0);
- (iv) proportions of females that exhibited spermatozoa in vaginal smears by day 7 after male introducing (including only the individuals who survived to day 7);
- (v) latency until the occurrence of spermatozoa in smears;
- (vi) proportions of females known to conceive within 1 week after male introduction.

The proportions were compared with a Fisher exact test. The significance of the differences in latency until vaginal perforation was tested using one-way ANOVA with Tukey's HSD tests for the post-hoc comparisons. A Student *t*-test was used to compare the latency until the occurrence of spermatozoa in smears in D daughters and MD mothers (the sample size for MD daughters was insufficient for the statistical comparison).

Based on weekly inspections of female vaginal condition from the second week after introduction of the male until the onset of their first pregnancy or until the death, we calculated the percentage of days with perforated vaginas for each female. This characteristic was used to compare the reproductive condition through the experiment for three categories of females. Only the females with minimum eight non-pregnant registrations were included into this analysis. The statistical significance of the effect of female category on this variable was estimated with the one-way

ANOVA. Post-hoc comparisons were performed using Tukey's HSD tests.

High mortality observed in MD groups (see Results) made statistical comparison of birth rate between treatments meaningless. We used a Wilcoxon matched pairs test to compare the likelihood of breeding between mothers and daughters in those MD groups that persisted until the appearance of at least one litter. We provide the information on breeding activity of dead individuals based on the results of necropsies. Dates of copulations were revealed retrospectively, based on the dates of parturition and the gestation period of about 30 days (Smorkatcheva et al., 2016). Intervals until birth of the first litter in MD mothers and D daughters were compared with a non-parametric Mann-Whitney *U* test.

We used a Fisher's exact test to compare the proportion of D and MD groups in which all members survived to the end of the experiment. For the groups with mortality, we estimated whether daughters were more likely to die than the mothers with a Binomial test. We used a multiple linear regression to analyze relationships between duration of group persistence (dependent variable) and female age and body condition. The group persistence was determined as the time from male introduction until the death of any group member or, for the groups without deaths, until the end of the experiment (180 days). The predictors were: daughter's and maternal ages, daughter's and maternal body masses, mother-daughter age difference, and mother-daughter body mass difference, all determined at the day of male introduction. To avoid the confounding effect of the time period, this factor was also included into the model as a categorical variable (3 levels = 3 experimental sets). The correlations among the predictors were previously tested with Pearson's correlation analysis.

All tests were two tailed and the α level of significance was 0.05.

Results and discussion

By the end of the experiment all individuals in 15 D groups were alive whereas mortality was observed in eight of 12 MD groups (a Fischer exact test: $p < 0.001$). Of them, the daughters died in six groups and the mothers died in two groups (a Binomial test: $p = 0.289$). In fact, with our small sample size and low power of this analysis (0.368), we can not rule out effect of female category on the likelihood to die. The details relevant for the interpretation of the observed mortality are given below in the context of reproductive data.

"Early" deaths and female reproductive activation during the first week after male introduction

Two MD daughters died on days 1 and 4 after male introduction. One of them was found dead with her fingers bitten of. Another daughter was observed sitting outside of the common nest with a slight (unlikely lethal) wound on her belly; she died two days afterward. The exact causes of these deaths are unknown. We speculate that they were associated with the sudden rise of the mother's intolerance triggered by cohabitation with a male (Bowler et al., 2002). No agonistic interactions among group members were registered, but we could miss the short duration aggression. Necropsies of these two females revealed no signs of reproductive activity (no corpora lutea, no visible follicula, immature uteri).

Most of the females had closed vaginas on the day of male introducing, and female category did not affect the proportion of perforated individuals (Table 1; $p = 0.182$ – 1.000). All females excluding one MD daughter displayed vaginal perforation within the next seven days. There was a significant effect of the female category on the latency until vaginal perforation ($F_{2,23} = 11.2$;

Table 1

Reproductive characteristics recorded for different categories of female Zaisan mole voles after strange male introduction. D – pairs, MD – matrilineal trios.

Female category and treatment	Daughters, D	Mothers, MD	Daughters, MD
Proportion of females with open vaginas on the day of male introduction	5/15	4/12	1/12
Proportion of females perforated within 7 days after male introduction ^a	10/10	8/8	8/9
Latency until vaginal perforation, days, X ± SD (n ^a)	2.9 ± 0.78 (10)	2.1 ± 0.90 (8)	5.0 ± 1.73 (8)
Proportion of females that displayed spermatozoa in vaginal smears within seven days after male introduction ^b	5/15	9/12	2/10
Latency until occurrence of spermatozoa in vaginal smears, days, X ± SD (n)	4.60 ± 0.55 (5)	3.78 ± 1.39 (9)	4.5 (2)
Percentage of days with open vaginas, X ± SD (n ^c)	44.5 ± 22.5 (12)	42.7 ± 24.1 (4)	18.3 ± 17.7 (8)
Interval from pairing to birth of litter, medians/lower and upper quartiles (n)	101/68–138 (9)	43/35–126 (7)	47 (1)

^a Number of the females that had closed vaginas on day 0, survived for at least seven days, and displayed vaginal perforation during this period.

^b Denominator represents the number of females that survived until the day 7.

^c Number of the females with minimum number of non-pregnant registrations = 8.

$p = 0.005$). This period was longer in MD daughters than in D daughters or MD mothers (Table 1; $p = 0.005$ and $p < 0.001$, respectively).

The vaginal smear analysis revealed the absence of intra-individual fluctuations or inter-individual differences in cell types or percentages of cell types. We never observed the cytological patterns that could be categorized as vaginal proestrus (predominance of the parabasal or intermediate epithelial cells) or estrus (predominance of the nonnucleated cornified cells, no leucocyte). Nucleated cells, if any, were always present in only a small number. Virtually all smears, including those taken on the days of copulation or before copulation, contained a combination of leucocytes and cornified cells. This was true for the smears taken on the days of successful impregnations as well (30 ± 1 days before the delivery). There was no consistent relationship between the presence or absence of spermatozoa and the proportion of cornified cells.

Most of mothers, including the mothers of two early dead daughters, displayed spermatozoa in vaginal smears during the first week after group formation whereas most of daughters did not (Table 1). The proportion of the inseminated mothers differed significantly from that of MD daughters ($p = 0.030$) and marginally from that of D daughters ($p = 0.054$). In addition, mothers tended to display shorter latency until spermatozoa in smears than D daughters ($t = 1.97$; $df = 12$; $p = 0.073$). D and MD daughters were quite similar in both the proportion of inseminated individuals and the latency until spermatozoa in smears (Table 1). Of 9 mothers who copulated, one displayed spermatozoa for three consecutive days, three displayed spermatozoa for two days and each of other five females – only once. Both D and MD daughters that displayed spermatozoa did so only once. Apparently neither D nor MD daughters conceived within the first week after male introduction, but four MD mothers did (significance of differences, a Fischer exact test: D daughters vs MD mothers: $p = 0.028$; MD daughters vs MD mothers: $p = 0.093$).

Taken together, these results suggest that in *E. tancrei* the presence of a mother did not completely prevent but somewhat delayed the onset of daughter's reproductive activation. In a closely related cooperative species, *Microtus pinetorum*, most of the daughters housed with a strange male in the presence of their mother did not ovulate and had lower uterine masses than the daughters in pairs. In this species, daughters from matrilineal groups did not respond to male exposure by increase in LH and were less attractive for a male than their mothers (Solomon et al., 2001). As in pine voles, the reproductive delay in our mole vole daughters may be due to the suppressive physiological influence by the older female, to the deficiency of the male-related stimuli (the possible consequence of the male choice and higher attractiveness of an older/experienced female), or both. On the other hand, D daughters significantly delayed copulations and conceptions, in comparison with MD mothers, despite being housed in the absence of the older females. This finding appears to parallel the age-related differences in sexual behavior and fertility reported for female gray-tailed voles, *Microtus canicaudus*. In this species, the younger females

exhibited lesser propensities to display receptive behavior, higher incidence of sterile matings, and, as a result, lower pregnancy rate than the older females (Petersen, 1986). We assume therefore that the reproductive skew in matrilineal groups of *E. tancrei* was initially generated by an age or experience asymmetry rather than, or in addition to dominance asymmetry.

Female reproductive activity throughout the experiment and "late" deaths

Female category affected the percentage of days with open vaginas (Table 1; $F_{2,22} = 4.0$; $p = 0.032$). MD daughters displayed perforated vaginas less frequently than the females of other categories. Post-hoc analysis revealed the significant difference between MD and D daughters (Table 1; $p = 0.030$); the difference between non-pregnant MD mothers and MD daughters was insignificant probably due to a small number of mothers included into the analysis.

Births occurred in nine D groups and in seven MD groups. In MD groups the mothers were significantly more likely to give birth than the daughters: only mothers delivered in six groups and both females delivered in one group (Wilcoxon matched pairs test: $Z = 2.20$; $N = 7$; $p = 0.028$).

In the only group with plural breeding, the mother delivered 12 days prior to the delivery of her daughter. Both litters died (disappeared) on the first-second day of life. The interval from pair formation until birth of litter was significantly longer in D daughters than in MD mothers (Table 1; $Z = 2.64$; $p = 0.038$).

Only four MD groups persisted until the end of the experiment. "Late" deaths occurred 29–137 days after group formation. Daughters died in two of six groups with mother's breeding, in the only group with plural breeding, and in one non-breeding group. Three of four dead MD daughters had *corpora hemorrhagica* in their ovaries, suggesting ovulation having occurred shortly before the death. Although voles are generally referred as induced ovulators (Hasler, 1975; Seabloom, 1985), intra- and interspecies differences in the amount and sources of stimuli which may provoke *corpus luteum* formation have been reported (Ferguson et al., 1984). Therefore, the findings of *corpora lutea* in the female mole vole did not reliably indicate recent copulations. Mothers died in two of three non-breeding groups. In one of these groups, the dead mother had fresh *corpora lutea* in the ovaries but had no visible embryos. In the second group, the dead mother was non-reproductive while the daughter was retrospectively revealed to conceive near the day of the mother's death. Thus, five MD daughters actually attempted to breed. The ages at breeding attempts in these females (269 ± 25 days, $n = 5$) closely coincided the conception ages retrospectively determined for the delivering D daughters (270 ± 50 days, $n = 9$). Therefore, whereas the comparison of vaginal condition between D and MD young females indicated some socially-mediated reproductive suppression, the data on birth rate and ovaries condition of the dead females provided no reliable evi-

dence for the role of the physiological suppression in constraining the breeding of MD daughters.

Immediate causes of the “late” deaths were unclear. Based on the time association, a causal link between the periods of the young females’ receptivity and “late” deaths is plausible. These deaths may be the consequences of contesting the mother’s reproductive monopoly by the daughters. However, none of the dead animals had visible injuries, suggesting that the deaths unlikely resulted from direct aggression but rather from some stress-related diseases or autonomic disorders (see Firestone et al., 1991 for the similar phenomenon in *M. ochrogaster* and Sgoifo et al., 1999; Bartolomucci, 2007; Wood et al., 2009; Beery and Kaufer, 2015 for reviews of the negative consequences of social stress in rodents). Apparently, the lethal outcomes we observed were the artifacts of confinement housing. In nature, they could be prevented by the forced or voluntary emigration of a subordinate.

Variation of MD groups persistence in relation to female ages and body masses

The correlation analysis for seven potential predictors of group persistence revealed very strong positive correlations between maternal age and maternal-daughter age difference ($R=0.98$; $p < 0.001$) and between daughter’s body mass and mother-daughter difference in body mass ($R=0.86$; $p < 0.001$); all other independent variables were uncorrelated. To avoid the colinearity and to make the model simpler we first performed the multiple regression analysis without characteristics of mother-daughter asymmetry, and then repeated the analysis replacing maternal age by age difference and daughter’s body mass by mass difference. Both regression models were significant ($F_{5,6} = 11.7$; $p = 0.005$), explained 83.0% of the variation in the output and yielded essentially the same results, so we provide the statistics for only the first one. The group persistence was associated positively with maternal mass ($t = 2.75$; $p = 0.033$) and maternal age/age difference ($t = 4.45$; $p = 0.004$), and negatively with daughter’s age ($t = -3.85$; $p = 0.009$). Daughter’s body mass/mother-daughter difference in mass showed no relationship to group persistence ($t = 1.30$; $p = 0.241$). The additional model which did not include daughter’s body mass confirmed the significant effects of both mother’s characteristics and daughter’s age. The results remained the same when two MD groups with “early” deaths were excluded from the analysis.

Two non-alternative causes may explain the influence of the maternal body mass on the tenacity of MD groups. First, poor physical condition of dominant animal may be associated with a low level of dominance and increased likelihood that the reproductive monopoly will be contested with the lethal outcome for one of the competitors. Another possible explanation is that the mothers in poor condition were less tolerant toward the younger conspecifics. This second scenario is more consistent with the lack of association between group persistence and asymmetry in mass/daughter’s body mass and with high incidence of daughter’s deaths.

Age is another individual characteristic known to determine social hierarchy and the output of the reproductive conflict in animal groups (Korona, 1991; Creel et al., 1992; Clarke and Faulkes, 1998; Clutton-Brock et al., 2006; Hodge et al., 2008; Nichols et al., 2012; Šárová et al., 2013). In the pine vole, *Microtus pinetorum*, a species with predominantly singular breeding system, the likelihood that the younger (subordinate) of two females housed with a strange male will be bred was positively associated with the age of subordinate, and negatively with the age asymmetry or the dominant’s age (Solomon et al., 2006). Our data for *E. tancrei* do not allow us to test directly the relationship between MD daughter’s reproductive activity and any individual characteristic. However, we know that (i) the latency until a death of MD females was negatively associated with the age of a daughter, and positively with

the age asymmetry or the age of a mother; (ii) none of the survived MD daughters bred or displayed signs of pregnancy, and (iii) most of the deaths occurred about the time when young females were receptive. Based on these facts we suppose that the same factors affect the level of reproductive suppression in the pine vole and Zaisan mole vole, and that the influence of females’ ages on group persistence in our experiment was mediated by the reproductive activity of the subordinates.

The age-related increase in reproductive attempts of subordinate females has been described for several cooperatively breeding mammals apart of voles (*Helogale parvula* – Creel and Waser, 1997; *Leontopithecus rosalia* – Baker et al., 2002; *Suricata suricatta* – Young et al., 2006, *Callithrix jacchus* – Abbott et al., 2009) and thus seems to be a widely occurring phenomenon. Ultimately, this tendency can be explained by the diminishing likelihood to obtain a dominant breeding position during the dwindling lifespan. In a species with mainly intrinsic mortality (what is apparently true for highly subterranean mole voles and may be also true for semi-subterranean pine voles), the survival probability should decrease with individual’s age, enhancing the value of current vs future reproduction. The younger female competitor can afford to wait for the breeding vacancy longer than the older one (Rowley and Russell, 1990; Kokko and Johnstone, 1999; Abbott et al., 2009). Based on the same argument one can expect a positive association between the dominant female’s age and the effort she invests in the maintenance of her status. From the subordinate point of view, the age of a dominant may predict the duration of social queuing until acceding to dominant status. For a daughter of an old mother with a short life expectancy, the best option may be just to wait as a loyal non-breeder for a breeding vacancy. In contrast, for a daughter or a sister of a relatively young dominant either attempts to contest the established dominance or dispersal and attempts to breed independently may be more advantageous. Additionally or alternatively, both subordinate and dominant efforts in the reproductive competition may be conditioned by age asymmetry if it indicates reliably the differences in resource-holding potential (RHP). If two individuals show little or no difference in age/RHP, it may benefit the subordinate to challenge the dominant for reproductive status (Solomon et al., 2006). However, in fully grown Zaisan mole voles such as we used in our experiments body mass is not related to age, and the positive correlation between age and RHP (fighting ability) is doubtful.

It remains to be revealed whether in the Zaisan mole vole two sisters of the same age are able to breed communally or not; we predict that such trios are unstable due to female–female antagonism. The results of several studies which have examined rodents’ reproductive skew with similar methods show that the sharing of reproduction vary from egalitarian to despotic in matrilineal groups whereas little or no skew usually occurs in groups containing female litter-mates (deer mice, *Peromyscus* – Haig, 1987; *Microtus ochrogaster* and meadow vole, *M. pennsylvanicus* – Wolff et al., 2001; wood mouse, *Apodemus sylvaticus* – Gerlach and Bartmann, 2002; mandarin vole, *Lasiopodomys mandarinus* – Smorkatcheva (transliterated in this article) 2002; Smorkatcheva and Orlova, 2011; social vole, *M. socialis* – Zorenko, 2013). This suggests that the dependence of the skew level on the dominant’s age demonstrated for *M. pinetorum* may be a widespread phenomenon. Testing this hypothesis is of great interest as if true, it might explain some intra-species and possibly even interspecies contrasts in social/breeding systems by just demographic differences.

General conclusion

The results of this experiment show that in *E. tancrei* the replacement of an original sire in a matrilineal group by a new male almost

never leads to the onset of plural breeding. In a newly formed family, a young/virgin female requires longer period of cohabitation with a male than does an older/sexually experienced female to successfully conceive. This difference may generate and maintain a skew for one or two months which, in some populations of mole voles, may actually last until the end of the reproductive season (Shubin, 1978a). Subsequently, one of two scenarios may happen: either the mother's reproductive monopoly is not challenged and trio persists as a cooperative group, or the females become intolerant to each other, eventually resulting in death (in captivity) or emigration (in field) of the loser. The weaker (in terms of body mass) and the younger (in terms of the absolute age, or in relation to the age of the daughter) is a mother, and the older is a daughter, the less stable is a trio. We assume that the relationships between group tenacity and females' ages may be mediated by the inhibitory effect of a mother on daughter's reproductive activity. Even if the subordinate female occasionally succeeds to gestate in the presence of her mother, the offspring probably will not survive due to infanticide. The combination of the listed factors makes the plural reproduction in matrilineal families of *E. tancrei* very unlikely. Additional experiments are required to estimate the relative importance of the behavioral and physiological suppression and inbreeding avoidance in constraining breeding of daughters in this species, and to test the effect of the dominant's age on the level of reproductive inhibition.

The available data for other voles living in family groups suggest that the death intolerance between female relatives is an unusual trait of *E. tancrei*. Many vole species have been reported to successfully rear their litters communally (narrow-headed vole, *Stenocranius gregalis* and steppe lemming, *Lagurus lagurus* – Shubin, 1978b,c; California vole, *M. californicus* – Ostfeld, 1986; common vole, *Microtus arvalis* – Boyce and Boyce, 1988; Brandt's vole, *Lasiopodomys brandtii* – Zöphel, 1999; Gromov, 2003, see also the references above). Although in some species a polygyny is associated with the reduced reproductive success due to delay of breeding, infanticide or impaired maternal care (Solomon et al., 2006; Smorkatcheva and Orlova, 2011), we are unaware of any examples of high adult mortality in groups comprising kin females. High incidence of lethal outputs in our experiment indicates an extremely strong female–female competition in the Zaisan mole vole in nature. In this regard *E. tancrei* appears to be more similar to a subterranean hystricognath species, the Damaraland mole-rat, *Fukomys damarensis* (Cooney and Bennett, 2000), than to the studied non-subterranean arvicoline living in groups. On the other hand, the occurrence of plurally breeding groups in the northeastern population of the sibling species, *E. talpinus* (Novikov et al., 2007) demonstrates that the subterranean specialization does not necessarily result in despotic reproductive monopoly. Broad variation among closely related species/populations of mole voles provides a unique opportunity to test the role of ecological and demographical factors for the evolution of the reproductive skew, and to reveal the proximate mechanisms underlying the shift from the singular to communal breeding.

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