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No asymmetry in the level of incest avoidance between mother–son and father–daughter pairs in the mandarin vole (*Lasiopodomys mandarinus*) (Rodentia: Arvicolinae)

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ABSTRACT. Animals of most species avoid close inbreeding, but the levels of incest avoidance (IA) vary both between and within species. Evolutionary reasons for this diversity are generally unclear. Comparison of IA between closely-related species and between within species categories (sexes, age classes or categories of kin pairs) could provide important tools to test hypotheses on the evolution of IA strategies. In this laboratory study we compared the likelihood of reproduction between mother–son and father–daughter pairs in a monogamous subterranean vole, *Lasiopodomys mandarinus*. The subterranean lifestyle is associated with impeded mates' encounters, costly dispersal, and relatively low value of each breeding attempt, which factors are expected to restrain the IA evolution. In polygynous uniparental animals, the predominance of father–daughter inbreeding over mother–son inbreeding is predicted. We aimed to test whether *L. mandarinus*, which exhibits a partial reversal of sex roles, displays an opposite pattern of asymmetry with a weakened IA between a mother and a son. Against the expectation, reproductive performance was dramatically reduced in both kin combinations. Mandarin vole's IA strategies follow the pattern typical for non-subterranean species with strong pair bonding, supporting the importance of mating system for IA evolution.

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KEY WORDS: *Lasiopodomys mandarinus*, voles, asymmetrical incest avoidance; mating choice; social control of reproduction.

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Уровень избегания инбридинга китайскими полевками (*Lasiopodomys mandarinus*) (Rodentia: Arvicolinae) в парах мать-сын и отец-дочь не зависит от характера родства партнеров

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РЕЗЮМЕ. Большинство видов животных избегает тесного инбридинга, однако уровень толерантности к инцесту варьирует как между видами, так и внутри одного вида. Эволюционные причины такого разнообразия неясны. Сравнение степени избегания инбридинга (ИИ) у близкородственных видов и внутривидовых категорий (разных полов, возрастных классов и вариантов родственных пар) может быть полезно для тестирования моделей эволюции ИИ. В этом лабораторном исследовании мы сравнили вероятность размножения в парах мать–сын и отец–дочь у *Lasiopodomys mandarinus*, моногамной полевки, специализированной к подземному образу жизни. Подземный образ жизни связан с затрудненным поиском половых партнеров, высокой ценой дисперсии и сравнительно низкой ценой каждого акта размножения, что в целом должно ослаблять отбор в пользу ИИ. Для полигинных млекопитающих без существенного отцовского вклада теоретически предсказано более частое размножение в парах отец–дочь, чем в парах мать–сын. Целью нашей работы было проверить, проявляет ли *L. mandarinus*, вид с частичной реверсией половых ролей, противоположный паттерн, т.е. ослабленное ИИ между матерью и сыном. Вопреки ожиданиям, размножение было подавлено в обоих типах близкородственных пар. Таким образом, стратегия избегания инбридинга у китайской

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полевки следует паттерну, типичному для неподземных видов с устойчивыми парные связями и бипарентной заботой. Этот результат подтверждает важность системы спаривания для эволюции избегания инбридинга.

КЛЮЧЕВЫЕ СЛОВА: *Lasiopodomys mandarinus*, полевки, асимметрия в избегании инбридинга, выбор партнера, социальный контроль размножения.

Introduction

The view that most animal species display strong tendencies to avoid mating with relatives as it can lead to inbreeding depression is widely held. Sex-biased natal dispersal, reproductive suppression, lack of reproductive activation in the absence of an unrelated mate, or refusal of a reproductively active animal to mate with a relative are several non-exclusive to one another ways to avoid inbreeding (Greenwood *et al*., 1978; Pusey, 1987). However, empirical evidence shows that incest avoidance (IA) is not a universal phenomenon (de Boer *et al*., 2021 for review). The evolutionary reasons for the revealed differences are generally unclear. The natural selection might not support IA due to limitations in effective kin recognition, low population density and high costs of dispersal (Kokko & Ots, 2006; Parker, 2006; Szulkin *et al*., 2013; Duthie & Reid, 2015; Pillay & Rymer, 2017; de Boer *et al*., 2021). Moreover, the cost-benefit ratio of IA can be affected by the sex, age, relationship, or social status of an individual, creating a precondition for the asymmetry in inbreeding tolerance between kin partners as well as between maternal and paternal kin pairs (Waser *et al*., 1986; Haig, 1999; Parker, 2006; Wheelwright *et al*., 2006; Lemaître *et al*., 2012). Generally, mother-son inbreeding is expected to be rarer than father-daughter inbreeding for the following two reasons. First, the cost of incest in terms of missed outbred mating is usually higher for females than for males due to their higher parental investment. Thus, females are expected to be more averse to incest than males (Waser *et al*., 1986; Haig, 1999; Parker, 2006; Duthie & Reid, 2015). In cases where the ages of potential sexual partners are different, sexual conflict is generally more likely to be resolved in favor of older individuals as they tend to be larger and/or more dominant (Waser *et al*., 1986; Haig, 1999). Second, in polygamous species (and those in which extra-pair copulations are common) a father and a daughter identify each other with greater uncertainty than a mother and a son, and errors in kin recognition may hinder the evolution of active incest avoidance mechanisms (Hatchwell, 2010; Galezo *et al*., 2022). Surprisingly, the predicted difference in the likelihood of inbreeding between mother–son and father–daughter pairs have been largely untested. The respective data are available for a negligible number of species but they suggest that the above theoretical considerations may not be applicable to all species. The pattern described for human (*Homo sapiens* Linnaeus, 1758), baboons (*Papio cynocephalus* Linnaeus, 1766 and *Papio anubis* Lesson, 1827) and Brandt's vole (*Lasiopodomys brandtii* Radde, 1861) is consistent with the expectation (Haig, 1999; Zorenko & Kaprale, 2003; Galezo *et al*., 2022). However, in some birds, breeding in mother-son pairs was noted more often than in father-daughter pairs, apparently due to their kin discriminating mechanisms (Wheelwright *et al*., 2006). Among mammals, two subterranean rodents have been reported to display weaker incest avoidance between mother and sons than between father and daughters (Ansell's mole-rat, *Fukomys anselli* — Burda, 1995, 1999; Zaisan mole vole, *Ellobius tancrei* Blasius, 1884 — Smorkatcheva, 2021). Clearly, variation in demography, mate fidelity, reproductive physiology, constraints on natal dispersal and kin recognition may affect differences in incest avoidance levels as a function of sex, age and relationship. Comparison of IA between closely-related species and between within species categories (sexes, age classes or categories of kin pairs) provide important tools to test hypotheses on the evolution of IA strategies.

The rodent subfamily Arvicolinae Gray, 1821 (Cricetidae) is an ideal model for studying adaptive evolution of various characteristics, including IA. Voles are relatively similar in morphology, life history, and physiology, but occupy various habitats, form fluctuating or stably sparse populations, and exhibit diverse social and mating systems. Importantly, these animals readily reproduce in captivity and have short life cycles, which facilitate their use in laboratory experiments designed to compare breeding success of outbred and related pairs. It has been shown that voles, as many other animals, rely primarily on learning prior association during the early ontogeny period to identify close relatives (Gavish *et al*., 1984; Boyd & Blaustein, 1985; Berger *et al*., 1997; Getz & Carter, 1998; Lucia & Keane, 2012; but see Tai *et al*., 2002; Kruczek, 2007). Reproductive performance of kin and non-kin pairs was compared under laboratory conditions in twelve species of voles (Batzli *et al*., 1977; Mcguire & Getz, 1981; Facemire & Batzli, 1983; Schadler, 1983; Bollinger *et al*., 1991; dos Santos *et al*., 1995; Tai *et al*., 2002; Zorenko & Kaprale, 2003; Smorkatcheva, 2021; Streltsov & Smorkatcheva, 2021). In most studied species, reproduction between conspecifics that were intimately associated during infancy is suppressed to some degree. Several mechanisms (delay of sexual maturation, mate choice and non-fertile mating) can reduce likelihood of inbreeding (Berger *et al*., 1997; Getz & Carter, 1998; Tai *et al,* 2002; Kruczek, 2007). Importantly, the level of IA varies among vole species being very strong in most socially monogamous voles with prolonged pair-bonding and pronounced paternal care (Zorenko & Kaprale, 2003; Smorkatcheva, 2021). This agrees well with theoretical expectations because in these species both sexes would forfeit outbreeding mating by choosing kin as a partner. However, weakened IA has been reported for monogamous Zaisan mole voles (*E. tancrei*), highly specialized subterranean arvicolines (Smorkatcheva, 2021). This finding is also consistent with the theory: subterranean lifestyle is associated with impeded mates' encounters, risky or energetically expensive dispersal, and relatively low value of each breeding attempt (Nevo, 1979; Stein, 2000; Burda, 2007) which should increase the cost-benefit ratio of the IA (Kokko & Ots, 2006; Parker, 2006; Duthie & Reid, 2015). In *E. tancrei*, as mentioned above, mother–son pairs were most likely to reproduce, whereas father-daughter pairs displayed strong IA (Smorkatcheva, 2021). Smorkatcheva linked this pattern to a partial reversal of sex roles as indicated by the female-biased dimorphism in size (Davydov, 1988) and aggressiveness (Smorkatcheva, unpublished). It has been suggested that pairing with relatives leaves more opportunities to obtain better partners for females than for male mole voles.

Mandarin voles (*Lasiopodomys mandarinus* Milne-Edwards, 1871) live in extended-family communal groups. Both male and female offspring often continue to live within natal group after reaching the age of sexual maturity (Smorkatcheva, 1999). The mandarin vole exhibits characteristics of subterranean rodents in behavior, demographics, physiology, and genome evolutionary tendencies (Smorkatcheva *et al*., 1990; Smorkatcheva, 2001; Liu *et al*., 2013; Sun *et al*., 2018; Bondareva *et al*., 2021; Dymskaya *et al*., 2022). Due to the limitations of the subterranean lifestyle, *L. mandarinus* occupies highly fragmented habitats and occurs at low population densities, by arvicoline standards, at least in the Northern part of the species range (Dmitriev, 1980; Smorkatcheva, 2001). These features imply high costs of mate search and suggest that the mechanisms preventing inbreeding may be somewhat weakened in this species. Further, *L. mandarinus* is similar to *E. tancrei* in prolonged pair bonding, delayed natal dispersal, reversed size dimorphism and higher female aggressiveness (Smorkatcheva, 1998, 1999, 2003b; Smorkatcheva *et al*., 2010). The last two features, indicating a partial reversal of sex roles, may reflect intense reproductive competition between females for limited and slowly renewing underground food. According to our laboratory data, males not only display direct parental care, but perform most of energetically expensive work, tunnel construction and bringing food and nest material (Smorkatcheva, 2003a). Mated male mandarin voles are subjected to severe aggression from their female partners and may even be killed after close contact with a strange female (Smorkatcheva, unpublished). On the other hand, in nature, wandering males were observed to visit the territory of a family group (Smorkatcheva, 1999), which may give females the opportunity for extra-pair copulations. These observations, together with demographic data, may suggest an asymmetrical IA similar to that of *E. tancrei*, i.e., weaker IA displayed by mother–son pairs than by other combinations of kin. Previous experiments with mandarin voles have shown that close inbreeding involving inexperienced females is highly unlikely and that kin recognition is based on both familiarity through association and phenotype matching mechanisms (Tai *et al*., 2002). The aim of this study was to estimate the reproductive performance exhibited of mother-son pairs, in comparison with father-daughter pairs.

Materials and methods

The study was performed at Saint Petersburg State University. The subjects were F 1–4 laboratory born voles, the descendants of 8 males and 12 females caught in Dzhidinsky (N104.5763º, E50.6361º) and Selenginsky (N104.935º, E50.896º) districts of Buryatia Republic, Russia. The distances between trapping sites ranged from 200 m to about 100 km, making the kinship of the lab colony founders very unlikely. Subsequently breeding pairs were established considering pedigree to exclude inbreeding. Family groups (a pair with offspring from one or two litters) were housed in glass terraria 50×25×30 cm^3), filled by one-third with wooden shaving. We provided the animals with wooden nest boxes and toilet paper as nesting material. Voles were fed *ad libitum* with carrots, apples, and a mix of oats, oat seedlings and rabbit pellets. The colony room was maintained at a temperature of 20–22°C, and on a 16 : 8 h light-dark cycle.

When the voles intended for use in this study were 30 days old, they and their parents were randomly assigned to one of four social conditions: a daughter with her father (DAD, n = 13), young female with an adult male from another family (NDAD, n = 17), a son with his mother (MUM, n = 13), or a young male with an adult female from another family (NMUM, n = 9). Same-sex siblings were randomly assigned to different social conditions. The study groups then remained intact until the young subjects were 52–77 days of age (X ± SD: DAD female: 60 ± 4; NDAD females: 59 ± 6; MUM males: 60 ± 3; NMUM males: 60 ± 3). These ages were set based on the minimum age of fertility reported for male and female mandarin voles (55 and 36, respectively, Zorenko *et al*., 1994). On Day 0 of the experiment, all groups were divided so as to separate male and female breeders. DAD and MUM pairs were established. Unweaned (24 days or younger) juveniles, if present, were left with dams. Outbred pairs were established on Day 4 by pairing young voles assigned to NDAD and NMUM treatments with an unfamiliar adult of the opposite sex. Thus, for the first four days the subjects in outbred treatments were in various social conditions, but always not in a full family. A short period of isolation from the previous partner or natal group prior to pairing was necessary because in *L. mandarinus* the members of established pairs, especially adult females, are often highly aggressive toward strangers of either sex. Mean (± SD) ages of the adult members of DAD, NDAD, MUM and NMUM groups were 292 ± 100 days, 284 ± 89 days; 259 ± 105 days and 185 ± 24 days. *L. mandarinus* is a relatively long-living species of voles, and these ranges of ages correspond to the period of full physical maturity and high reproductive activity. Differences in the age of older individuals between related and unrelated pairs were insignificant. At the beginning of the experiment, one of NMUM females and three of MUM females were obviously pregnant. Two of NMUM females and five of MUM females had unweaned offspring.

Immediately before pairing, all voles were weighed to the nearest 0.1 g. At pairing, a male and a female were put into a clean terrarium. Housing conditions were as described above. Thereafter, we examined and weighted the females weekly for pregnancy detection. We used steady weight gain, prominent nipples and vaginal bleeding as indicators of pregnancy. Nests of the females in the late period of pregnancy were examined daily. All pairs were monitored for 90 days since pairing, which is more than three times the gestation period and three times the average latency to the first birth (22.7 days and 33 days, respectively (Smorkatcheva, 1998). Such a long duration ensured that even if the unequal initial conditions influenced the reproductive success, it would affect the latency to the birth rather than probability of reproduction. Pups born after the 24th day of the experiment were considered the offspring of the new pairs.

We compared the proportions of dead individuals between inbred and outbred treatments. The groups in which at least one animal died before the birth of offspring were excluded from further analyses. We compared the proportions of pairs producing joint litters between DAD and NDAD, between MUM and NMUM, and between DAD and MUM treatments. A Fisher's exact test was used in these analyses. Duration of intervals from pairing to birth of the first litter was compared with a Mann–Whitney U test. All tests were two-tailed, the level of significance was $\alpha = 0.05$. Given small sample sizes, odds ratios (OR) are provided in addition to the results of the Fisher's exact tests. OR is a measure of effect size when comparing proportions of a categorical outcome according to different independent groups. As general rules of thumb, OR > 3.0 for positive associations and OR < 1/3 for negative associations indicate strong relationships (Sullivan & Feinn, 2012; Ialongo, 2016).

All applicable international, national and institutional guidelines for the care and use of animals were followed. The study was approved by the Bioethics Committees of the Saint Petersburg State University, SPbU #131–03–2.

Results and discussion

Two NDAD females, one MUM male, one MUM female, three DAD males and one DAD female died during the experiment, yielding 4% and 12% mortality in outbred and inbred treatments, respectively ($p = 0.270$; OR = 3.4). The animals died on days 6–59 of the experiment. They had no wounds, and the exact causes of these deaths are unknown. Given our small sample size, the detrimental effect of the prolonged living with a kin mate cannot be rule out.

Nine NMUM pairs (100%) and 13 of 15 survived NDAD pairs (87%) produced at least one joint litter ($p = 0.510$; OR = 3.1). Again, the lack of statistical significance may be due to small sample sizes. The latency to the birth did not differ significantly between NDAD and NMUM treatments (median and 25% quartiles): 31 (29–42) and 37 (30–47) days, respectively (U = 47; $p = 0.460$; n1 = 9; n2 = 13). Three of 11 MUM females gave birth, but only one of these litters was conceived from a son (latency 31 days). In this case, no newborns were found, and the delivery was inferred from the female's weight dynamics and nipples condition. In another MUM female, bloody vaginal discharge without significant weight gain was recorded which may indicate a failed pregnancy. None of females from DAD groups gave birth or displayed any sign of pregnancy. The proportions of pairs that produced joint litters significantly differed between inbred and outbred treatments ($p < 0.001$ for both MUM vs NMUM and DAD vs NDAD), whereas there was no difference between MUM and DAD treatments ($p > 0.999$; OR = 2.7).

In this study of *L. mandarinus*, the reproductive performance was dramatically reduced in both mother–son and father–daughter pairs at a level comparable to that previously shown for siblings of this species (Tai *et al.*, 2002). Inbreeding depression could make some contribution to the decrease in the reproductive success of kin pairs, and the design of this study, like most similar studies before it, did not disentangle influences of this factor and IA. However, the origin of the founders of our laboratory colony and the strategy of its maintenance ensures that the individuals participating in this experiment were not inbred themselves. According to available data, the effect of inbreeding depression on the first inbred generation is rather weak and is manifested as a decrease in offspring growth rate or survival rather than early losses of all embryos (e.g., dos Santos *et al.*, 1995; Bixler & Tang-Martinez, 2006; Pillay & Rymer, 2017).

Strong IA between young females and their fathers was expected, given the results of former experiments and what is known about the reproductive activation in young female mandarin voles (Tai *et al.*, 2000; 2002; Smorkatcheva, 2003b). The most probable mechanism preventing incestuous reproduction in DAD groups is a failure of young females to come into estrus in the absence of an unrelated (unfamiliar) male (Tai *et al.*, 2002). Based on the ecological and behavioral similarities between *L. mandarinus* and *E. tancrei*, we hypothesized that IA may be weakened in mother-son pairs. The results did not confirm our assumption. Our experiment was not designed as to discriminate between the possible proximate causes of reproductive failure in mother-son pairs. Several mechanisms seem to prevent this type of incestuous breeding in a closely-related species, prairie vole (*Microtus ochrogaster* Wagner, 1842).

In this species, the reproductive activity of young males was suppressed by stimuli from their mother, father or siblings. The activation of the suppressed males after the exposure to unrelated females may take several days to occur, the activated males rarely copulate with their mother during her postpartum estrus period, and if they did, the mating were not fertile (Getz & Carter, 1998). We speculate that these same mechanisms, most probably based on the pheromonal effects, may complement each other in the mandarin vole.

Among the species characteristics that may affect costs-benefits ratio of IA, the costs of mate search and the level of iteroparity seem to differ strikingly in mole voles and mandarin voles. First, *Ellobius* Fischer, 1814 has prominent morphological adaptations to underground existence which should make mate search particularly costly, in terms of risk, energy, or both (Stein, 2000). Less specialized mandarin vole does not appear to differ much from other voles in its ability to move on the ground. Second, mole voles stand out among all other arvicolines by their exceptional iteroparity with a female reproductive life span of up to six years even in nature (Evdokimov, 2001 for *Ellobius talpinus* Pallas, 1770). The respective published data for *L. mandarinus* are not available, but in the wild, only 1 of 143 marked mandarin voles was trapped the next breeding season (Smorkatcheva, unpublished), suggesting the typical "arvicoline" life history with a short life span and a relatively high investment per each litter. Differences between *E. tancrei* and *L.mandarinus* in life history and dispersal costs may explain different IA strategies in these species.

Most of the similar studies on other vole species quantified only IA between siblings or, rarely, between father and daughter (Batzli *et al*., 1977; Mcguire & Getz, 1981; Facemire & Batzli, 1983; Schadler, 1983; Boyd & Blaustein, 1985; Bollinger *et al*., 1991; Streltsov & Smorkatcheva, 2021), but there are a few exceptions. Two monogamous species are known to exhibit strict IA in all combinations of relatives (*M. ochrogaster* — Getz & Carter, 1998; social vole, *Microtus socialis* Pallas, 1773 — Zorenko & Kaprale, 2003). In contrast, only mother-son pairs strongly avoid incest in polygamous Brandt's voles, *L. brandtii* (Zorenko & Kaprale, 2003). Thus, despite some unusual features of the ecology and behavior of the mandarin vole, its IA strategies follow the pattern typical for species with pair bonding, supporting the importance of mating system for IA evolution.

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