

Parental care in the captive mandarin vole, *Lasiopodomys mandarinus*

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Abstract: Based on the social structure of free-living mandarin voles (*Lasiopodomys mandarinus*), high paternal investment might be expected for this species. This prediction was tested under laboratory conditions. We observed 10 pairs rearing their first litter. All pairs exhibited permanent nest cohabitation. Females never prevented males from entering the natal nest. Males exhibited all the patterns of direct care of young except nursing: huddling over, brooding with kyphosis, grooming, manipulating, and retrieving young. There were no sex differences in total time spent in the nest or in time spent alone. Females spent more time grooming pups than did males. There was no sex difference in nest-building activity. The frequency of bringing food or nest material into the nest, as well as in digging time, was significantly greater for males than for females. In *L. mandarinus* the biparental rearing system with a high level of direct paternal care and some division of labour between the parents seems to be associated with the subterranean mode of life. This pattern of parental care can be predicted for other specialized fossorial voles.

Résumé : La structure sociale des campagnols mandarins (*Lasiopodomys mandarinus*) en nature fait croire que l'investissement du père doit être élevé. La prédiction a pu être vérifiée en laboratoire. Dix couples ont été observés lors de l'élevage de leur première portée. Tous les couples cohabitent au nid de façon permanente. Les femelles n'empêchent jamais les mâles d'entrer dans le nid natal. Les mâles font toutes les fonctions de soins des petits, sauf l'allaitement: regrouper les petits, les couvrir le dos en bosse, faire leur toilette, les manipuler et les rattraper. Il n'y a pas de différence entre les sexes, quant au temps total passé au nid et au temps passé seul. Les femelles passent plus de temps à toiletter les petits que ne font les mâles. Il n'y a pas de différence entre les sexes dans les activités de construction du nid. Les mâles passent significativement plus de temps que les femelles à transporter de la nourriture ou des matériaux dans le nid et à creuser. Chez *L. mandarinus*, le système d'élevage des petits qui implique les deux parents, avec des soins paternels importants et une certaine division du travail entre les parents, semble être associé à la vie souterraine. On peut prédire que le même type de soins parentaux existe chez d'autres campagnols fouisseurs spécialisés.

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Introduction

During the last few decades, parental care in mammals has received increasing attention from ethologists, ecologists, and physiologists. The subfamily Arvicolinae is an ideal group of rodents for comparative studies in this area (Dewsbury 1990; Wang and Insel 1996; Lonstein and DeVries 2000). Sex or species differences in this behaviour, as well as in the proximate mechanisms underlying them, in voles have become topics for a large body of research. However, these investigations have involved only a few members of the vast subfamily Arvicolinae. Quantitative data are available for five species of the genus *Microtus* (Hartung and Dewsbury 1979; Thomas and Birney 1979; Wilson 1982; McGuire and Novak 1984; Gruder-Adams and Getz 1985; Oliveras and Novak 1986; Storey and Snow 1987; McGuire

1988; Solomon 1993; Wang and Novak 1994; Lonstein and DeVries 2000), the collared lemming, *Dicrostonyx richardsoni* (Shilton and Brooks 1989; Gaida and Brooks 1993), the red-backed vole, *Clethrionomys gapperi* (McGuire 1997), and the sagebrush vole, *Lemmys curtatus* (Hoffmann et al. 1989). Additionally, I and my co-workers were able to find some observational data on parental care in a few Palearctic species (Pegelman 1977; Zorenko 1983; Fernandez-Salvador et al. 2001). For most species of voles, information on parental behaviour is lacking. Meanwhile, to reconstruct the evolution of arvicoline social systems, social traits as well as ecological specialization in a number of species representing different taxa must be known and compared.

The mandarin vole, *Lasiopodomys mandarinus*, is a specialized member of the subfamily Arvicolinae distributed throughout the grasslands of Central Asia. It leads an almost completely subterranean existence and digs extensive tunnel systems to forage for geophytes as well as aerial parts of plants (Dmitriev 1980; Smorkatcheva et al. 1990; Smorkatcheva 2001). During the reproductive period, mandarin voles live in extended family groups. In southern Siberia in summer, groups typically consist of one breeding male, one to five breeding females, and one to three generations of young (Smorkatcheva 1999). In the Chinese population of mandarin voles, monogamous families and communal groups in-

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cluding several adult males and females have been reported (Tai and Wang 2001). Group territoriality is likely and mateships are prolonged (Smorkatcheva 1999).

Based on the social structure of free-living mandarin voles, high paternal investment can be suggested. Indeed, the preliminary observations made by our group showed that the male is involved in parental care (Zorenko et al. 1994). The goal of this study was to describe parental behaviour and compare the amounts of direct as well as indirect parental care provided by captive male and female mandarin voles at different stages of the rearing period.

Material and methods

Animals and housing

The animals used in these experiments were laboratory-reared descendants of stock originally captured in Buryatia (southern Siberia) in 1990–1994. All animals were maintained on a 16 h light : 8 h dark photoperiod (lights on at 0700). Carrots, oats, and hay were provided ad libitum. In addition, small amounts of oat shoots, willow twigs, and sunflower seeds were provided. The hay served as both food and nest material. Voles were housed in glass aquaria (25 cm × 50 cm × 30 cm) half-filled with wood shavings. When the female was nearing parturition (3–4 d prior to the birth of a litter), a clean wooden box (18 cm × 34 cm × 20 cm) was put into the same aquarium. The space between the glass and the walls of the box was filled with wood shavings. This space was 3.5 cm wide on the long sides (“tunnels”) and 8 cm wide on the short sides (“chambers”, one of which was used by the voles as a nest chamber). The design allowed animals to demonstrate a broad set of behaviours and provided them with the opportunity to nest separately. I could observe all the activities of the animals in the tunnels and most of their activities in the chambers.

Immediately before a pair was introduced into an observation cage, the fur on both sides of the male was cut to allow identification.

Behavioural observations

I observed 10 pairs rearing their first litter. Each family group was observed on day 2 after the birth of the young (day 0 = day of birth) and thereafter every 1–2 d, for 1 h each time (between the hours of 2100 and 2300 or between the hours of 0900 and 1100). I did not include day 1 in the schedule because at that time the behaviour patterns of the parents are often modified by postpartum oestrus of the female. The times at which each adult entered and left the nest were recorded. This information was used to calculate the total time spent in the nest and the time spent alone in the nest by the male and female. I also recorded the following behaviours for each parent: duration of pup grooming; frequency of pup retrieval; frequency of manipulating nest material while in the nest; frequency of bringing nest material (hay or wood shavings) into the nest; frequency of bringing other objects (carrot, seeds, pieces of twig, grass blades) into the nest; and duration of building and maintaining burrow tunnels (digging, scratching, carrying out debris).

Data analysis

Observational data were grouped into four pup stages: 2–6, 7–11, 12–16, and 17–21 d, with three observation sessions per stage period for each pair. Interactions between sex, stage, and time of day (morning or evening) were analysed using $2 \times 4 \times 2$ factorial ANOVA. Since not all the variables were distributed normally, Wilcoxon’s two-sample test was used to assess the significance of differences between the sexes (for each pup stage as well as for the entire rearing period) and between pup stages (for each sex). In that case, the mean for the three observation sessions was calculated, to provide an average value for each rearing period for each parent and behaviour. Statistical significance in all cases was $p < 0.05$.

Results

Repertoire of parental behaviours

All pairs exhibited permanent nest cohabitation. Females never prevented males from entering the natal nest. The repertoire of parental behaviours displayed was essentially identical for mothers and fathers. Males exhibited all the patterns of direct care of young except nursing: huddling over, brooding, grooming, manipulating, and retrieving young. When brooding, both male and female mandarin voles displayed a specific posture resembling kyphosis (upright crouched nursing/huddling posture) (Lonstein and DeVries 1999) and ventral trembling. Males contributed to nest building and maintenance: they pushed up or pulled out wood shavings and hay, closed the nest entrance after the female departed, and brought material to the nest. They also engaged in tunnel building and maintenance as well as food hoarding.

Relative amounts of parental care provided by males and females

There were no significant interactions between any factors (sex, pup stage, time of day) for any behaviours (Table 1).

Nest residence

There were no sex differences in the total time spent in the nest or the time spent alone over the whole observation period (see Table 2). Though females were in the nest more than males at pup stage 2–6 d (the difference was almost statistically significant; $z = 1.78$, $p < 0.07$), this difference disappeared as the pups became older (Fig. 1). For females the time spent in the nest at pup stage 2–6 d was slightly greater than at pup stage 7–11 d ($z = 1.83$, $p < 0.07$) and significantly greater than at pup stages 12–16 d ($z = 2.55$, $p < 0.01$) and 17–21 d ($z = 2.19$, $p < 0.03$). There were no changes in time spent alone in the nest by females with age of pups. In contrast, for males the total duration of nest residence did not change over time, whereas time spent alone in the nest with pups 2–6 d old was less than with the older pups (2–6 vs. 7–11 d; $z = 1.72$, $p < 0.09$; 2–6 vs. 12–16 d; $z = 2.40$, $p < 0.02$; 2–6 vs. 17–21 d; $z = 2.09$, $p < 0.04$).

Grooming

Females spent more time grooming pups than did males. This difference was significant for the entire observation period (Table 2) as well as for all pup stages except 17–21 d (Fig. 1). The time devoted to grooming by females declined slightly from pup stages 7–11 to 17–21 d ($z = 2.20$, $p < 0.03$;

Table 1. Interaction effects (*p* values) between sex, pup stage, and time of day for captive mandarin voles, *Lasiopodomys mandarinus*.

Behaviour	Sex × stage	Sex × time	Stage × time	Sex × stage × time
Nest residence ^a	0.202	0.742	0.921	0.824
Nest residence alone ^a	0.210	0.763	0.996	0.872
Pup grooming ^a	0.136	0.169	0.828	0.273
Manipulation of nest material ^b	0.747	0.731	0.321	0.574
Bringing objects to the nest (total) ^b	0.679	0.879	0.360	0.284
Bringing nest material only ^b	0.772	0.822	0.376	0.216
Bringing food only ^b	0.594	0.993	0.554	0.450
Tunnel maintenance ^a	0.692	0.905	0.777	0.293
Tunnel maintenance ^c	0.732	0.830	0.678	0.595

^aMean duration.^bMean frequency.^cMean proportion of time spent out of the nest.**Table 2.** Behavioural comparisons between female and male mandarin voles during pup rearing.

Behaviour	Females	Males	<i>z</i> score	<i>p</i>
Nest residence ^a	2928 ± 68	2822 ± 112	0.47	0.642
Nest residence alone ^a	655 ± 94	554 ± 61	0.40	0.693
Pup grooming ^a	169 ± 22	65 ± 14	3.48	0.001
Manipulation of nest material ^b	0.5 ± 0.1	0.3 ± 0.1	1.29	0.201
Bringing objects to the nest (total) ^b	0.3 ± 0.1	2.4 ± 0.6	3.23	0.001
Bringing nest material only ^b	0.1 ± 0.02	0.8 ± 0.03	2.78	0.005
Bringing food only ^b	0.2 ± 0.1	1.6 ± 0.5	3.07	0.002
Tunnel maintenance ^a	205 ± 43	353 ± 72	2.01	0.052
Tunnel maintenance ^c	25.6 ± 3.94	36.9 ± 4.47	2.11	0.034

^aDuration (s) per 1-h period (mean ± 1 SE).^bFrequency (number of occurrences per 1-h period; mean ± 1 SE).^cPercentage of time spent out of the nest (mean ± 1 SE).

the remaining differences were not significant). In males this measure increased slightly from stages 2–6 to 12–16 d (Fig. 1); all differences were nonsignificant.

Retrieving young

The data pertaining to retrieval of young were not statistically analysed because this behaviour was very infrequent in both females and males. Of 51 instances of retrieval that I and my co-workers observed, 27 (53%) were performed by females and 24 by males. Most instances (26/51 or 51%) occurred on the first days that young were recorded out of the nest, at pup stage 12–16 d.

Nest maintenance

Manipulating nest material in the nest was observed infrequently. There were no sex differences in the frequency of this behaviour for the entire rearing period, nor for any of the pup stages (Table 2, Fig. 2). There were no significant differences in females' or males' nest-building activity between any two pup stages.

Bringing objects into the nest

Males brought carrot and seeds, as well as hay, 8 times as often as females did during the whole observation period (Table 2). When instances of bringing food and nest material were pooled, there were statistically significant sex differences for all pup stages except 7–11 d (Fig. 2). There were

no differences in the frequency of bringing objects between any two pup stages for females or males.

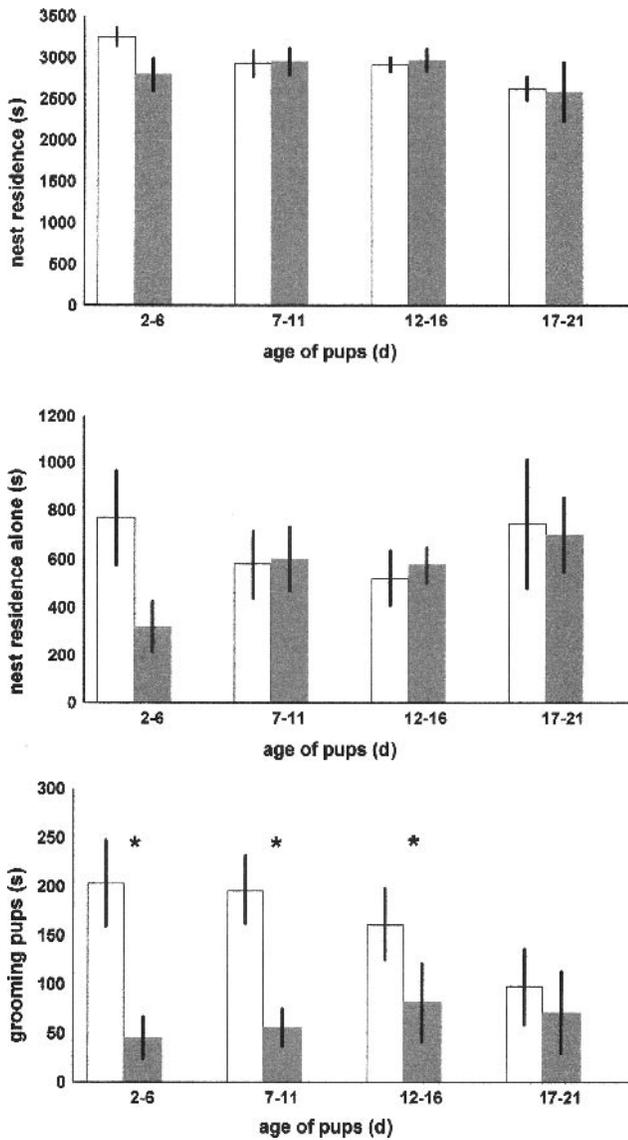
Tunnel construction and maintenance

Males spent more time digging, scratching, and carrying out debris than females did over the entire observation period and in the first pup stage (Table 2, Fig. 3). For the remaining pup stages, sex differences did not reach statistical significance, though the tendency was the same (Fig. 3). It is interesting that males spent more time and a greater proportion of their activity (out of the nest) on this behaviour than did females. This difference was significant only for the entire rearing period (Table 2), but again the trend was the same at all pup stages (Fig. 3). There were no significant changes in this behaviour category for males or females.

Discussion

In this study, permanent nest cohabitation of pair members, similarity of the paternal behaviour repertoire to the maternal one, and a large amount of paternal care were observed. Both parents brooded, groomed, and retrieved pups and built the nest. Males as well as females displayed kyphosis. The time spent in the nest by the father was the same as that spent by the mother. Moreover, in some observed cases the female died and the father continued brooding the

Fig. 1. Time spent on direct parental care of pups of different ages by female (open bars) and male (shaded bars) mandarin voles, *Lasiopodomys mandarinus* (*, significant sex difference ($p < 0.05$)). Error bars represent 1 SE.



pups for several days (A.V. Smorkatcheva, unpublished data).

To my knowledge, among Arvicolinae the kyphosis of males observed in mandarin voles has so far been described only for the prairie vole, *Microtus ochrogaster*. The amount of direct parental behaviour provided by male as well as female mandarin voles was similar that observed for monogamous *M. ochrogaster* in small cages (Solomon 1993; Wang and Nowak 1994). For example, in my study, the duration of nest residence by males and females constituted about 78% and 81% of observation time, respectively. From the above-mentioned studies of male and female *M. ochrogaster*, I calculated values of about 92% and 96% (Solomon 1993) and about 78% and 79% (Wang and Novak 1994), respectively.

Thus, the results of this study of voles in captivity are consistent with field evidence of prolonged mateships (Smorkatcheva 1999; Tai and Wang 2001). Based on both

Fig. 2. Manipulation of nest material in the nest and bringing of objects into the nest by female (open bars) and male (shaded bars) mandarin voles at different ages of pups. Instances of bringing food and nest material are totaled (*, significant sex difference ($p < 0.05$)). Error bars represent 1 SE.

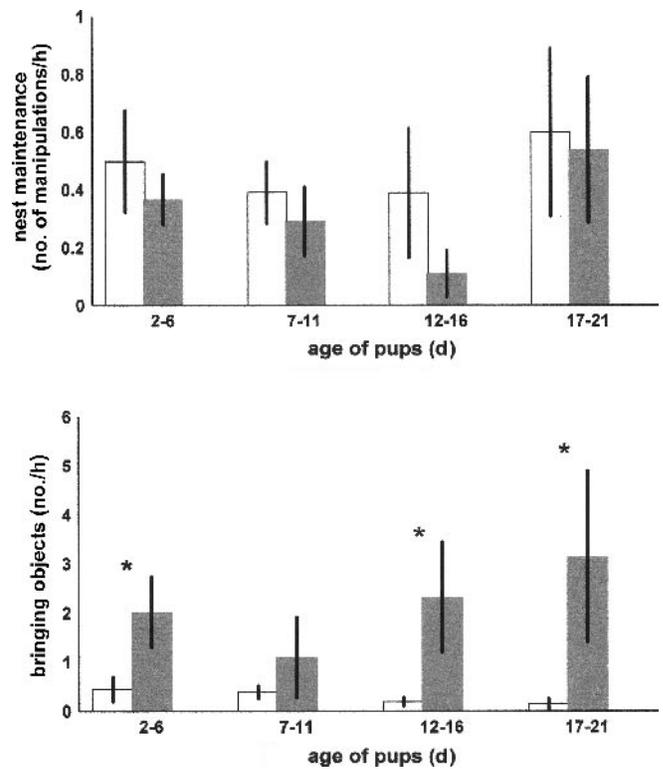
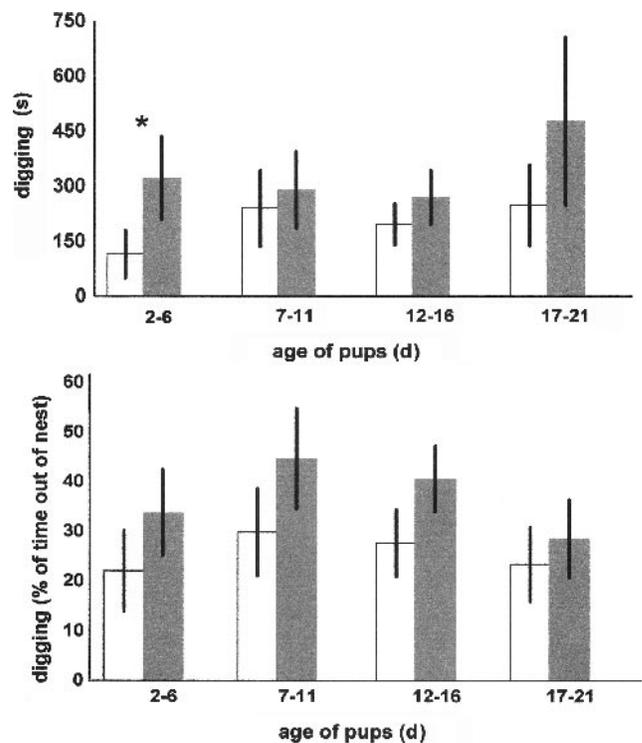


Fig. 3. Time spent on tunnel construction by female (open bars) and male (shaded bars) mandarin voles at different ages of pups (*, significant sex difference ($p < 0.05$)). Error bars represent 1 SE.



field and laboratory data, *L. mandarinus* seems to be a species that provides biparental care.

In my experiments the frequency of bringing food or nest material into the nest was significantly greater for male than for female mandarin voles. Males seem to provide food to both young (at pup stage 12–21 d) and lactating females (at pup stage 2–6 d). Moreover, males contributed more than females to burrow construction and maintenance. Thus, the indirect parental investment by fathers was greater than by mothers. Unfortunately, information on the distribution of indirect care between the sexes is often not available in the literature: in most investigations attention has been focused on direct parental behaviour. In the studies of McGuire and Novak (1984) and Oliveras and Novak (1986), digging, food caching, and nest building were compared between four *Microtus* species but not between the sexes. Since those authors observed maternal (McGuire and Novak 1984) and paternal (Oliveras and Novak 1986) behaviours of the same species under similar conditions, using their values for a between-sex comparison appeared to be of interest. Such a comparison shows that the time spent on tunnel construction was greater for female than for male meadow voles, *Microtus pennsylvanicus* (in the case of meadow voles, none of the parents cached food). In contrast, both the durations and frequencies of food caching and tunnel construction were somewhat greater in male than in female pine voles, *Microtus pinetorum*, as well as prairie voles. However, Solomon (1993) found no sex differences in indirect parental care in prairie voles. Apparently, the only arvicoline in which division of labour between the sexes has been reported, with the male playing the major role in providing offspring with food, is the muskrat, *Ondatra zibethica* (Marinelli and Messier 1995).

Of course, the conclusion that males perform most of the work in mandarin vole families should be tested under conditions more similar to those in the wild. Nevertheless, this finding should attract the attention of future investigators to the distribution of indirect paternal investment in other vole species. Cross-species comparisons may help us to understand the ecological correlates and ultimate mechanisms underlying the evolution of biparental care in voles.

In general, we can expect to see biparental care supported under two conditions: (1) the benefits of seeking out additional mates are relatively low (Emlen and Oring 1977; Dewsbury 1985) and (or) (2) the benefits of remaining with the female and caring for young are relatively high. Examples of monogamous voles displaying biparental care are generally considered to be exceptional (Wolff 1985; Nelson 1987) and have been explained by very different ecological factors. For example, the social system of the prairie vole is believed to be an adaptation to homogeneous, stable, low-food habitats where the females are widely dispersed and the costs of searching for other mates are high (i.e., condition 1 is fulfilled) (Getz and Carter 1996). In the muskrat, extended paternal care is likely associated with the large size of adults and, consequently, the slow growth of juveniles, which are not able to live independently by the time their mother gives birth to the next litter (i.e., condition 2 is fulfilled) (Marinelli and Messier 1995). In the mandarin vole, both conditions seem to be fulfilled, owing to their subterranean mode of life: (i) As one might expect for a fossorial rodent, which

uses stable but limited resources, the mandarin vole is a *K*-selected species, and its population density is typically low (Dmitriev 1980; Smorkatcheva 2001). The costs of above-ground as well as underground wandering must be high for a subterranean rodent, especially in an open environment. The search for additional mates is likely to be complicated (condition 1). (ii) Apparently, like most voles, the mandarin vole is a poor digger. Though the species is *K*-selected among arvicolines, its reproductive ratio is high in comparison with other subterranean rodents. During the reproductive period most females produce several litters successively (Smorkatcheva 1993, 1999). Litter mass at birth constitutes, on average, about 20% of maternal mass (A.V. Smorkatcheva, unpublished data). Energy requirements should be much higher for breeding than for nonbreeding females, as has been proved for other species (Kaczmarski 1966; Gebczynski 1984). Female mandarin voles, which combine pregnancy with lactation and have to obtain food by excavating soil, are likely faced with a severe energetic problem. The problem cannot be solved by using fat reserves, because voles do not store fat. The performing of most of the energetically expensive activities by the male might result in improving the female's physical condition, increasing her productivity and (or) longevity. Thus, indirect parental care should contribute to both the present and the future offspring of the same female (condition 2).

The similar arguments have been put forward by Burda (1990) to explain the evolution of monogamy as well as eusociality in Bathyergidae. According to this argument, the biparental rearing system and the major role of the male in digging and foraging should be characteristic of any vole species specialized for a subterranean mode of life. Actually, based on field data, at least two fossorial species, the mole vole *Ellobius talpinus* (Zubko and Ostryakov 1961; Evdokimov 2001) and the pine vole (Fitzgerald and Madison 1983), appear to live in monogamous/polyandrous family groups. The scanty information on the mole vole *Promethomys schaposchnikovi* seems to support monogamy in this species too (Gambaryan et al. 1957). The data on the social organisation of the European pine vole, *Microtus subterraneus*, are contradictory (Langestein-Issel 1950; Salvioni 1988), but I do not expect it to be promiscuous. As far as I know, among these voles parental care has been investigated only in the pine vole (McGuire and Novak 1984; Oliveras and Novak 1986). In these studies, male pine voles have been shown to contribute to both direct and indirect parental care. Moreover, the comparison of the amounts of time spent in various behaviours by females (McGuire and Novak 1984) and males (Oliveras and Novak 1986) seems to provide evidence that in this species, the father's indirect parental investment is greater than the mother's, though females contribute more than males to brooding, grooming, and retrieving pups. Whether or not there really is some division of labour between the parents in this and other fossorial voles remains to be revealed.

Though alloparental behaviour of older offspring was not investigated in the current study, I will briefly touch on this subject. The high risk of aboveground wandering, the shortage of vacant tunnel systems, and the high cost of digging new tunnel systems should constrain natal dispersal and favour philopatry (Powell and Fried 1992; Solomon and Getz

1997). Apparently, this is the case for any subterranean vole. On the other hand, helping by philopatric offspring may be selected as an indirect fitness benefit. The assistance of older offspring in the care of pups has been reported for fossorial (pine vole, Powell and Fried 1992; Solomon and Getz 1997; mandarin vole, Zorenko et al. 1994) as well as non-fossorial (prairie vole, Solomon 1991) arvicolines. However, for a subterranean vole, the young may substantially increase the reproductive output of their mother by undertaking the most expensive (in terms of energy) part of the workload, i.e., digging.

Thus, though cooperative breeding is not specific to fossorial arvicolines, it is expected to be typical of all of them. I predict that in fossorial voles, older offspring contribute more than the breeding female to burrow construction. These propositions should be tested in both field and laboratory studies. An investigation of alloparental care in the mandarin vole is in progress.

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References

- Burda, H. 1990. Constraints of pregnancy and evolution of sociality in mole-rats with special reference to reproductive and social patterns in *Cryptomys hottentotus* (Bathiergidae, Rodentia). *Z. Zool. Syst. Evolutionsforsch.* **28**: 26–39.
- Dewsbury, D.A. 1985. Paternal behavior in rodents. *Am. Zool.* **25**: 841–852.
- Dewsbury, D.A. 1990. Individual attributes generate contrasting degrees of sociality in voles. In *Social system and population cycles in voles*. Edited by R.H. Tamarin, R.S. Ostfeld, S.R. Pugh, and G. Bujalska. Birkhauser-Verlag, Basel, Boston, and Berlin. pp. 1–10.
- Dmitriev, P.P. 1980. Ecology of the mandarin vole *Microtus mandarinus*, and its role in pasture biocoenoses of north Mongolia. *Zool. Zh.* **59**: 1852–1861. [In Russian.]
- Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science (Wash., D.C.)*, **197**: 215–223.
- Evdokimov, N.G. 2001. Population ecology of the mole-vole. Ural Branch of the Russian Academy of Science, Ekatherinburg, Russia.
- Fernandez-Salvador, R., Garcia-Perea, R., and Ventura, J. 2001. Reproduction and postnatal growth of the Cabrera vole, *Microtus cabreræ*, in captivity. *Can. J. Zool.* **79**: 2080–2085.
- Fitzgerald, R.W., and Madison, D.M. 1983. Social organization of a free-ranging population of pine vole, *Microtus pinetorum*. *Behav. Ecol. Sociobiol.* **13**: 183–187.
- Gaida, A.M., and Brooks, R.J. 1993. Paternal care in collared lemmings (*Dicrostonyx richardsoni*): artifact or adaptation? *Arctic*, **46**: 312–315.
- Gambaryan, P.P., Karapetyan, V.S., Airumyan, K.L., Kasaryan, K.T., and Mejlumyan, S.K. 1957. On the ecology of the Prometheus' mice. *Mater. Izuch. Fauny Arm. SSR Erevan.* **3**: 5–16. [In Russian.]
- Gebczynski, M. 1984. The energy cost of nesting growth in the European pine vole *Pitymys subterraneus*. *Acta Theriol.* **29**: 231–242.
- Getz, L.L., and Carter, C.S. 1996. Prairie-vole partnerships. *Am. Sci.* **84**: 56–62.
- Gruder-Adams, S., and Getz, L.L. 1985. Comparison of the mating system and paternal behavior in *Microtus ochrogaster* and *M. pennsylvanicus*. *J. Mammal.* **66**: 165–167.
- Hartung, T.G., and Dewsbury, D.A. 1979. Paternal behavior in six species of muroid rodents. *Behav. Neural Biol.* **26**: 466–478.
- Hoffmann, J.F., McGuire, B., and Pizzuto, T.M. 1989. Parental care in the sagebrush vole (*Lemmiscus curtatus*). *J. Mammal.* **70**: 162–165.
- Kaczmarek, F. 1966. Bioenergetics of pregnancy and lactation in the bank vole. *Acta Theriol.* **11**: 409–417.
- Langestein-Issel, B. 1950. Biologische und ökologische Untersuchungen über die Kurzhohrmaus (*Pitymys subterraneus* de Selys-Longchamps). *Pflanzenbau Pflanzenschutz.* **1**: 145–183.
- Lonstein, J.S., and DeVries, G.J. 1999. Comparison of the parental behavior of pair-bonded female and male prairie voles. *Physiol. Behav.* **66**: 33–40.
- Lonstein, J.S., and DeVries, G.J. 2000. Sex differences in the parental behavior of rodents. *Neurosci. Biobehav. Rev.* **24**: 669–686.
- Marinelli, L., and Messier, F. 1995. Parental-care strategies among muskrats in a female-biased population. *Can. J. Zool.* **73**: 1503–1510.
- McGuire, B. 1988. Effects of cross-fostering on paternal behavior of meadow voles (*Microtus pennsylvanicus*). *J. Mammal.* **69**: 332–341.
- McGuire, B. 1997. Influence of father and pregnancy on maternal care in red-backed voles. *J. Mammal.* **78**: 839–849.
- McGuire, B., and Novak, M. 1984. A comparison of maternal behaviour in the meadow vole (*Microtus pennsylvanicus*), prairie vole (*M. ochrogaster*) and pine vole (*M. pinetorum*). *Anim. Behav.* **32**: 1132–1141.
- Nelson, J. 1987. Social organization in voles. *Reprocentralen Lunds Universitet, Lund, Sweden.*
- Oliveras, D., and Novak, M. 1986. A comparison of paternal behaviour in the meadow vole *Microtus pennsylvanicus*, the pine vole *M. pinetorum* and the prairie vole *M. ochrogaster*. *Anim. Behav.* **43**: 519–526.
- Pegelman, S.G. 1977. Parental care in the muroid rodents. In *Povedenije mlekopitajuschikh*. Nauka, Moscow. pp. 70–83.
- Powell, R.A., and Fried, J.J. 1992. Helping by juvenile pine voles (*Microtus pinetorum*), growth and survival of younger siblings, and the evolution of pine vole sociality. *Behav. Ecol.* **3**: 325–333.
- Salvioni, M. 1988. Home range and social behavior in three species of European *Pitymys* (Mammalia, Rodentia). *Ecol. Sociobiol.* **22**: 203–210.
- Shilton, C.M., and Brooks, R.J. 1989. Paternal care in captive collared lemmings (*Dicrostonyx richardsoni*) and its effect on development of the offspring. *Can. J. Zool.* **67**: 2740–2745.
- Smorkatcheva, A. 1993. Population structure and reproduction of *Lasiopodomys mandarinus* in the Transbaical region. In *Proceedings of the 4th International Conference "Rodents and Spatium"*, Mikolajki, Poland, 24–28 May 1983. Institute of Ecology, Polish Academy of Science, Dziekanow n/Warsaw. p. 101.
- Smorkatcheva, A. 1999. The social organization of the mandarin vole, *Lasiopodomys mandarinus*, during the reproductive period. *Z. Saeugetierkd.* **64**: 344–355.

- Smorkatcheva, A. 2001. On the distribution and ecology of the mandarin vole *Lasiopodomys mandarinus* in Buryatia. Proc. Zool. Inst. Russ. Acad. Sci. **288**: 188–204. [In Russian.]
- Smorkatcheva, A.V., Aksenova, T.G., and Zorenko, T.A. 1990. The ecology of *Lasiopodomys mandarinus* (Rodentia, Cricetidae) in the Transbaical area. Zool. Zh. **69**: 115–124. [In Russian.]
- Solomon, N.G. 1991. Current indirect fitness benefits associated with philopatry in juvenile prairie voles. Behav. Ecol. Sociobiol. **29**: 277–282.
- Solomon, N.G. 1993. Comparison of paternal behavior in male and female prairie voles (*Microtus ochrogaster*). Can. J. Zool. **71**: 434–437.
- Solomon, N.G., and Getz, L.L. 1997. Examination of alternative hypotheses for cooperative breeding in rodents. In Cooperative breeding in mammals. Edited by N.G. Solomon and T.A. French. Cambridge University Press., New York. pp. 199–230.
- Storey, A.E., and Snow, D.T. 1987. Male identity and enclosure size affect paternal attendance of meadow voles, *Microtus pennsylvanicus*. Anim. Behav. **35**: 411–419.
- Tai, F., and Wang, T. 2001. Social organization of mandarin voles in burrow system. Acta Theriol. Sin. **21**: 50–56. [In Chinese.]
- Thomas, J.A., and Birney, E.C. 1979. Parental care and mating system of the prairie vole, *Microtus ochrogaster*. Behav. Ecol. Sociobiol. **5**: 171–186.
- Wang, Z., and Insel, T.R. 1996. Parental behavior in voles. Adv. Stud. Behav. **25**: 361–384.
- Wang, Z., and Novak, M.A. 1994. Parental care and litter development in primiparous and multiparous prairie voles (*M. ochrogaster*). J. Mammal. **75**: 18–23.
- Wilson, S.C. 1982. Parent–young contact in prairie and meadow voles. J. Mammal. **63**: 300–305.
- Wolff, J.O. 1985. Behavior. In Biology of New World *Microtus*. Spec. Publ. Am. Soc. Mammal. No. 8. pp. 340–372.
- Zorenko, T.A. 1983. Peculiarities of reproductive behaviour in the Brandt's vole. In Gryzuny. Materialy 6-go Vsesojuznogo Soveshchaniya. Nauka, Leningrad. pp. 259–261.
- Zorenko, T.A., Smorkatcheva, A.V., and Aksenova, T.G. 1994. Reproduction and postnatal ontogenesis of mandarin vole *Lasiopodomys mandarinus* (Rodentia, Arvicolinae). Zool. Zh. **73**: 120–129. [In Russian.]
- Zubko, Y.A., and Ostryakov, C.I. 1961. On the reproduction of mole-voles (*Ellobius talpinus* Pal.) in the south of Ukraine. Zool. Zh. **40**: 1577–1579. [In Russian.]