Relationship between the Social Structure and Potential Reproductive Success in Muroid Rodents (Rodentia, Myomorpha)

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Abstract—In many systematic groups of mammalian species, the evolution of sociality leads to the formation of large social groups (group-size evolution). In rodents, however, the most social species live in family groups consisting, as a rule, of a fairly small number of individuals. The family-group lifestyle of some terrestrial sciurids (Sciuridae) and voles (Microtus) results in fewer breeding adult females, a decreased litter size, and a longer time before the first reproduction. Statistical analysis of published data performed in this study showed that the transition to the family-group lifestyle leads to decreased potential reproductive success in many muroid rodents: females produce fewer litters and, consequently, fewer pups during the breeding season. However, the potential reproductive success in muroid rodents with a family-group lifestyle could be increased due to delayed offspring dispersal (who spend the severe winter period in family groups) and extensive cooperation in foraging and in defending their territory and food reserves, as well as in care-giving activities. It can be assumed that females of these species produce fewer offspring, yet of “better quality.” Ultimately, social rodent species may gain inclusive fitness benefits because of the higher fitness of their offspring as compared to solitary dwellers and gregarious species.

Keywords: muroid rodents, social organization, potential reproductive success
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INTRODUCTION

According to existing concepts, the evolution of societies is aimed at providing certain advantages to individuals uniting in groups (Alexander, 1974). In other words, a group lifestyle, which is inevitably associated with such negative factors as an exacerbation of intraspecific competition and an increase in the risk of the spread of infectious and parasitic diseases, nevertheless, should be associated with an increase in fitness, the measure of which is reproductive success (Wolff and Sherman, 2007).

In many taxonomic groups of mammals (including primates, carnivores, and ungulates), the evolution of sociality is directed towards the formation of large groups (group-size evolution) (Lee, 1994; Grove, 2012). However, in rodents, the most social species are those with family groups, which usually unite a relatively small number of individuals (Gromov, 2013, 2017). The family-group lifestyle of the majority of rodent species is characterized by long-lasting pair-bonds, active participation of males in raising offspring, and a complex social organization, which is expressed in a hierarchical system of relations, the distribution of behavioral roles, differentiation of reproduction, and widespread cooperation. In other words, the evolution of sociality in rodents is closely associated with the formation of a complex social structure and social organization (Blumstein and Armitage, 1998).

However, the increasing complexity of social organization, as was shown in some studies (in particular, on terrestrial sciurids (Sciuridae)), has an adverse effect on individual fitness, because the reproductive potential of the most social species decreases: the proportion of adult females participating in breeding decreases, the number of pups in litters decreases, and the age of females starting to breed for the first time increases (Blumstein and Armitage, 1998; Armitage, 2007). A decrease in the number of pups in litters was also noted in some species of voles of the genus Microtus (M. pinetorum and M. ochrogaster), which are characterized by a family-group lifestyle (Innes, 1978). In view of the above, a question arises as to whether a decrease in the reproductive potential is a consequence of the transition to a family-group lifestyle in other rodent species as well.

Analysis of published data shows that, in addition to large terrestrial sciurids (Cynomys spp. and Marmota spp.), as well as some species of the tribe Hystricomorpha, the family-group lifestyle is also typical of some representatives of muroid rodents (Gromov, 2008). No one has previously tested whether there is a relationship between social structure and reproductive
potential in these rodents. In this regard, in this study, an attempt was made to compare the reproductive potential in a number of Myomorpha species belonging to different categories of sociality (in other words, with different types of the spatial-and-ethological population structure, SEPS) (Gromov, 2008). In rodents, four main types of SEPSs can be distinguished: type I (solitary dwellers), type II (a system of aggregations of adult heterosexual individuals), type III (societies with weakly consolidated family groups), and type IV (societies with structured family groups). According to this classification, species with type IV SEPS are characterized by the most complex social structure and, therefore, are at the top of sociality.

MATERIALS AND METHODS

The material for this study was published data on the reproductive potential of 45 species of muroid rodents (Tables 1, 2), namely, the average number of litters per adult female in the breeding season and the average number of pups in a litter. Due to the heterogeneity of the published data (the number of litters, as well as the number of pups in the litter, varies in different sources), the arithmetic mean value of the parameters studied was taken as the basis for statistical analysis (shown in parentheses in Tables 1 and 2). On the basis of these data, an additional index was calculated—the average number of pups produced by the female during the breeding season, which was defined as the product of two values—the average number of pups in a litter and the average number of litters.

The data obtained were processed by statistical methods of analysis of variance (one-way ANOVA) and regression analyzes using Pearson’s correlation coefficient (Sokal and Rohlf, 1995).

RESULTS AND DISCUSSION

Analysis of variance of the data shown in Tables 1 and 2 allows us to postulate that there is a strong correlation between the types of SEPS (and, accordingly, the social structure) and the reproduction indices such as the average number of litters and the total number of pups produced by the female during the breeding season: for the first index, $F = 6.568$, $df = 3.41$, $p < 0.001$; for the second index, $F = 6.803$, $df = 3.41$, $p < 0.001$.

The results of the regression analysis are completely consistent with the results of ANOVA: in the series of species compared, upon the transition from type I SEPS to type IV SEPS, the number of litters of females, as well as the total number of pups produced by one female during the breeding season, decreases (Figs. 1, 2).

The regression equation for the first index (the average number of litters ($N$) per female) is expressed by the following formula: $N = 3.952 - 0.449x$ (1–4), where 1–4 is the SEPS type ($R = -0.54$, $F = 17.855$, $df = 1.43$, $p <0.001$).

The regression equation for the second index (the total number of pups ($N$) produced by one female during the breeding season) is expressed by the formula $N = 24.974 - 3.431x$ (1–4), where 1–4 is the SEPS type ($R = -0.56$, $F = 20.061$, $df = 1.43$, $p < 0.001$).

On the basis of the calculations, it can be asserted that, in the weakly social species with type I SEPS,
females during the breeding season produce, on average, 3.5 litters containing, on average, 21.5 pups. In the social species with type IV SEPS, these indices are 2.2 and 11.3, respectively.

Thus, the transition to the family-group lifestyle in muroid rodents, indeed, is associated with a decrease in reproductive potential: females produce fewer litters and, accordingly, fewer pups per breeding season.

A question arises as to whether the pattern revealed should be considered as evidence of a decrease in individual fitness during the transition to the family-group lifestyle? On the one hand, from a formal point of view, a drop in the reproductive potential inevitably indicates a decrease in individual fitness. However, this circumstance can be viewed from the other side. The dispersal of the offspring of individuals belonging to weakly social species takes place shortly after weaning (Anderson, 1989), and a significant part of the young die in the process of dispersal (Wolff, 1994; Solomon, 2003; Nunes, 2007; Solomon and Keane, 2007). Some of the successfully settled females produce offspring (usually, only one litter) at the end of the current breeding season, and others breed after wintering, which is survived by only part of individi-
Thus, in species with a low level of sociality, the proportion of successfully bred young individuals that appeared during one breeding season ultimately is low. It is very difficult to calculate this index more accurately. In any case, no such data for murid rodents were found in the available literature.

Conversely, in the species with a family-group social organization and delayed dispersal of young animals, the rates of reproductive success may be higher. This is favored by the delay in the dispersal of young animals that survive the harsh winter period in a family group, as well as by the widespread cooperation, including the protection of the territory from other conspecific individuals, foraging, protection of food reserves, and raising offspring, in which not only parents but also grown immature individuals from older litters take an active part (Gromov, 2013; Solomon and Keane, 2007). Under these conditions, the mortality of young animals is reduced to a minimum and, accordingly, the total fitness of breeding individuals increases.

In many species with a family-group social organization, the dispersal of the major part of the young individuals takes place only after the first wintering, and in some species of marmots (Marmota spp.) and beavers (Castor spp.), it takes place in the third or even fourth year of life (Barash, 1974; Suntsov, 1981; Dezhkin et al., 1986; Armitage, 2007). In this case, young individuals are prepared for dispersal and independent existence much better than in the species with early

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Table 2. Reproductive characteristics of social species

| Species                          | Average number of litters (per female) | Average number of pups in a litter (per female) | Source                                      |
|----------------------------------|----------------------------------------|--------------------------------------------------|---------------------------------------------|
| **Species with type III SEPS**   |                                        |                                                  |                                             |
| Peromyscus californicus          | 2.35                                   | 1.9                                              | Drickamer and Vestal, 1973; Gubernick and Teferi, 2000 |
| Meriones libycus                 | 3—4 (3.5)                              | 5.5—5.6 (5.6)                                   | Kolesnikov, 1935; Burdelov et al., 1993    |
| Lagurus lagurus                  | 2—3 (2.5)                              | 5.8                                              | Kryl’tsov, 1955; Shevchenko, 1963          |
| Microtus arvalis                 | 3—5 (4)                                | 4.6—5.6 (5.0)                                   | Bashenina, 1962, 1994                      |
| Microtus socialis                | 2—3 (2.5)                              | 3.1—5.1 (4.1)                                   | Zorenko et al., 1997; Kasatkin, 2002       |
| Microtus guentheri               | 2—3 (2.5)                              | 8.8                                              | Cohen-Shlagman et al., 1984                |
| Microtus gregalis                | 2—3 (2.5)                              | 9.2                                              | Prokop’ev and Vinokurov, 1986; Shubin, 1974|
| Microtus californicus            | 2—3 (2.5)                              | 4.4—5.0 (4.7)                                   | Innes, 1978; Nadeau, 1985                  |
| Microtus xanthognathus           | 1—2 (1.5)                              | 8.0—8.8 (8.4)                                   | Innes, 1978; Wolff and Lidicker, 1980      |
| Dicrostonyx torquatus            | 2—3 (2.5)                              | 6.7                                              | Mezhennyi, 1975; Mallory and Brooks, 1978  |
| Mus spicilegus                   | 1—5 (3)                                | 5.4—8.5 (7.0)                                   | Sokolov et al., 1990                       |
| **Species with type IV SEPS**    |                                        |                                                  |                                             |
| Rhombomys opimus                 | 2—3 (2.5)                              | 6.0—6.3 (6.2)                                   | Kambulin, 1941; Dubrovskii, 1978; Sokolov et al., 1983 |
| Meriones unguiculatus            | 2—3 (2.5)                              | 4.5—6.5 (5.5)                                   | Leont’ev, 1954; Khamaganov, 1954; Lapin, 1989|
| Meriones vinogradovi             | 1—3 (2)                                | 6.2                                              | Papanyan, 1973                            |
| Microtus ochrogaster             | 1—2 (1.5)                              | 3.6                                              | Innes, 1978                               |
| Microtus pinetorum               | 1—2 (1.5)                              | 1.0—3.2 (2.1)                                   | Valentine and Kirkpatrick, 1970; Innes, 1978; Nadeau, 1985 |
| Lasiopodomys brandti             | 2—3 (2.5)                              | 6.1                                              | Zorenko and Yakobsone, 1986; Chen and Shi, 2003 |
| Lasiopodomys mandarinus          | 1—3 (2)                                | 3.3                                              | Zorenko et al., 1994                      |
| Ellobius talpinus                | 1—2 (1.5)                              | 4.0—7.0 (5.5)                                   | Evdokimov, 2001; Yakimenko, 2004          |
| Ondatra zibethicus               | 1—3 (2)                                | 6.2                                              | Strautman, 1963; Kudryashov and Kudryashova, 1982 |
dispersal of young animals. Thus, it can be postulated that the species with a family-group social organization produce fewer offspring, yet of a “better quality.” The low mortality rate of young individuals in family groups and their delayed dispersal undoubtedly enhance the individual fitness. Eventually, the inclusive fitness (Hamilton, 1964) in the social species may be higher than in solitary dwellers. However, special studies are required to confirm this assumption.

**COMPLIANCE WITH ETHICAL STANDARDS**

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

**REFERENCES**

Alexander, R.D., The evolution of social behavior, *Annu. Rev. Ecol. Syst.*, 1974, vol. 5, pp. 325–383.

Anderson, P.K., Dispersal in Rodents: A Resident Fitness Hypothesis, Provo, UT: American Society of Mammalogists, 1989.

Armitage, K.B., Evolution of sociality in marmots: it begins with hibernation, in *Rodent Societies—An Ecological and Evolutionary Perspective*, Wolff, J.O. and Sherman, P.W., Eds., Chicago: Chicago Univ. Press, 2007, pp. 356–367.

Asdell, S.A., *Patterns of Mammalian Reproduction*, New York: Comstock, 1964, 2nd ed.

Asenov, G.A., To ecology of the gray hamster (*Cricetus migratorius* Schreber), *Ekologiia obyknovennoi polevki i nekotorye aspekty fiziologicheskih i evolyutsionnyh obshchestva* (Mammals of the USSR: Proceedings of the III Conference of the Theriological Society of the USSR), Moscow: Inst. Evol. Morfol. Zhivotn., 1982, vol. 1, p. 194.

Blumstein, D.T. and Armitage, K.B., Life history consequences of social complexity: a comparative study of ground-dwelling sciurids, *Behav. Ecol.*, 1998, vol. 9, pp. 8–19.

Boonstra, R. and Boag, P.T., A test of the Chitty hypothesis: inheritance of life-history traits in meadow voles *Microtus pennsylvanicus, Evolution*, 1987, vol. 41, pp. 929–947.

Burdelev, A.S., Basin, B.V., Dyagilev, S.V., Bityalov, Z.A., and Ageev, V.S., The Libyan gerbil in the Northern Balkhash region, *Byull. Mask. O-va Ispyt. Prir.*, Otd. Biol., 1993, vol. 98, no. 1, pp. 14–23.

Chen, G. and Shi, D., The reproductive parameters in the marked populations of Brand’s vole, *Acta Theriol. Sin.*, 2003, vol. 23, pp. 220–224.

Cohen-Shlagman, L., Yom-Tov, Y., and Hellwing, S., The biology of the Levant vole, *Microtus guentheri*, in Israel. I. Population dynamics in the field, *Mammal. Biol.*, 1984, vol. 49, pp. 135–147.

Daly, M., Behavioral development in three hamster species, *Dev. Psychobiol.*, 1975, vol. 9, pp. 315–323.

Dezhkin, V.V., D’yakov, Yu.V., and Safonov, V.G., *Bahr* (The Beaver), Moscow: Agropromizdat, 1986.

Drickamer, L.C. and Vestal, B.M., Patterns of reproduction in a laboratory colony of *Peromyscus*, *M. J. Mammal.*, 1973, vol. 54, pp. 523–528.

Dubrovsky, Yu.A., Peschanki i prirodnyaya ochagovost’ kozh- nogo leishmanioza (Gerbils and the Natural Loci of Skin Leishmaniasis), Moscow: Nauka, 1978.

Evdokimov, N.G., *Populiationnaya ekologiya obyknovennoi slepushonki* (Population Ecology of the Mole Vole), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2001.

Evtushenko, E.Kh., The morphoecological features of the wood mouse in the Krivoi Rog region, in *Mlekopitatishchие SSSR: materialy III s”ezda Vseoiuznogo teriolohicheskogo obschestva* (Mammals of the USSR: Proceedings of III Conference of the Theriological Society of the USSR), Moscow: Inst. Evol. Morfol. Ekol. Zhivotn., 1982, vol. 1, p. 194.

Feoktistova, N.Yu., *Khomyaichi roda Phodopus. Sistematika, filogeografiia, ekologii, fiziologii, povedenie, khimicheskaya kommunikatsiya* (Dwarf Hamsters of the Genus Phodopus: Systematics, Philogeography, Ecology, Physiology, and Chemical Communication), Moscow: KMK, 2008.

Gromov, V.S., *Prostranstvenno-etoalogicheskaya struktura populyatsii gryzunov* (The Spatial-and-Ethological Population Structure in Rodents), Moscow: KMK, 2008.

Gromov, V.S., *Zabota o potomstve u gryzunov: etologicheskie, fiziologicheskie i evolyutsionnye aspekty* (Parental Care in Rodents: Ethological, Physiological, and Evolutionary Aspects), Moscow: KMK, 2013.

Gromov, V.S., *Evolyutsiya sotsial’nosti u mlekopitatayuschih* (The Evolution of Sociality in Mammals), Moscow: KMK, 2017.

Grove, M., Space, time, and group size: a model of constraints on primate social foraging, *Anim. Behav.*, 2012, vol. 83, pp. 411–419.

Gubernick, D.J. and Tefeti, T., Adaptive significance of male parental care in monogamous mammals, *Proc. R. Soc. London, Ser. B*, 2000, vol. 267, pp. 147–150.

Hamilton, W.D., The genetical evolution of social behavior, *J. Theor. Biol.*, 1964, vol. 7, pp. 1–52.

Ilan, M., Aspects of the biology and ecology of the fat sand rat (*Psammomys obesus*) in Israel, *M. Sc. Thesis*, Tel-Aviv, 1984.
Innes, D.G.L., A reexamination of litter size in some North American microtines, *Can. J. Zool.*, 1978, vol. 56, pp. 1488–1496.

Kambulin, E.A., Some data on ecology of the great gerbil (*Rhombomys opimus*) in Kazakhstan and how to control it, *Gryzuny Bor'ba Nimi*, 1941, no. 1, pp. 95–149.

Karaseva, E.V., Some data on biology of the root vole collected by the capture-recapture method, *Vopr. Ekol.*, 1957, vol. 2, pp. 141–150.

Kasatkin, M.V., Some features of biology and the population structure of the social vole (*Microtus socialis*), in *Sb. Nauch. Tr. Gos. Biol. Muzeya im. K.A. Timiryazeva* (Collection of Scientific Papers of K.A. Timiryazev State Biology Museum), 2002, pp. 103–142.

Khamaganov, S.A., To the biology of the Mongolian gerbil in the Torey Lakes region, *Izv. Irkutsk. Nauchno-Issled. Protivovuchunn. Inst. Sib. Dal'nego Vost.*, 1954, vol. 12, pp. 150–155.

Kolesnikov, I.I., The Libyan gerbil: some materials to its biology, economic importance and control, *Tr. Sredneaziat. Gos. Univ.*, Ser. VIIa. *Zool.*, 1935, no. 19, pp. 1–31.

Kondrashkin, G.A., Some regularities of reproduction and population dynamics of the bank vole in the Volga River delta, *Vopr. Ekol.*, 1957, vol. 2, pp. 151–173.

Koshkina, T.V., The ecological differentiation of a species with the red-backed vole inhabiting the taiga of the Salair Mountains, *Acta Theriol.*, 1967, vol. 12, no. 11, pp. 135–163.

Koshkina, T.V., On the factors affecting the population dynamics of lemmings, *Fauna Ekol. Gryzunov*, 1970, no. 9, pp. 11–61.

Kryltov, A.I., On winter reproduction of muroid rodents in the Northern Kazakhstan, *Byull. Mosk. O-va Ispyt. Prir.*, *Otd. Biol.*, 1955, vol. 60, no. 2, pp. 1–8.

Kudryashov, V.S. and Kudryashova, L.M., Some peculiarities of the muskrat reproduction in the Oka River basin, in *Mlekopitaiushchie SSSR: materialy III s''ezda Vsesoiuznogo teriologicheskogo obshchestva* (Mammals of the USSR: Proceedings of III Conference of the Theriological Society of the USSR), Moscow: Inst. Evol. Morfol. Ekol. Zhivotn., 1982, vol. 1, pp. 230–231.

Kuznetsova, N.A., Mamina, V.P. and Karaseva, O.V., Reproductive biology and the extent of the reproductive isolation of lemmings (Lemmus, Rodentia, Cricetidae) inhabiting the Far East, *Zool. Zh.*, 1993, vol. 72, no. 12, pp. 138–145.

Lambin, N. and Krebs, C.J., Spatial organization and mating system of *Microtus townsendii*, *Behav. Ecol. Sociobiol.*, 1991, vol. 28, pp. 353–363.

Lapin, V.A., Reproduction and Postnatal Development of Gerbils, in *Feschanki – vazhnuye gryzuny aridnoi zony SSSR: materialy III Vsesoiuznogo soveshchaniya* (Gerbils as Important Rodents of the Arid Zone of the USSR: Abstracts of III All-Union Conference), Tashkent: Fan, 1989, pp. 118–123.

Lee, P.C., Social structure and evolution, in *Behavior and Evolution*, Slater, P.J.B. and Halliday, T.R., Eds., Cambridge: Cambridge Univ. Press, 1994, pp. 266–303.

Leont’ev, A.N., To the ecology of the Mongolian gerbil in the Buryat-Mongolian SSR, *Izv. Irkutsk. Nauchno-Issled. Protivovuchunn. Inst. Sib. Dal'nego Vost.*, 1954, vol. 16, pp. 78–84.

Mallory, F.F. and Brooks, R.J., Infanticide and other reproductive strategies in the collared lemming, *Dicrostonyx groenlandicus*, *Nature*, 1978, vol. 273, pp. 144–146.

Mezhennyi, A.A., Materials to ecology of muroid rodents of the tundra and forest tundra in the northern Yakutia, in *Materialy po ekologii melkikh mlekopitaiushchikh Subarktiki* (Materials to the Ecology of Small Mammals of the Subarctic Region), Novosibirsk: Nauka, 1975, pp. 53–118.

Mihok, S., Behavioral structure and demography of subarctic *Clethrionomys gapperi* and *Peromyscus manipulus*, *Can. J. Zool.*, 1979, vol. 57, pp. 1520–1535.

Moskvitina, N.S. and Suchkova, N.G., Some population features of reproduction of the red-backed vole under conditions of the Western Siberian Plain, *Tr. Nauchno-Isled. Inst. Biol. Biofiz. Tomsk. Gos. Univ.*, 1974, vol. 4, pp. 51–55.

Myers, P. and Masters, L.I., Reproduction by *Peromyscus manipulus*: size and compromise, *J. Mammal.*, 1983, vol. 64, pp. 1–18.

Nadeau, J.H., Ontogeny, in *Biological of New World Microtus*, Tamarin, R.H., Ed., Shippensburg, PA: American Society of Mammalogists, 1985, pp. 254–285.

Nunes, S., Dispersal and philopatry, in *Rodent Societies—An Ecological and Evolutionary Perspective*, Wolff, J.O. and Sherman, P.W., Eds., Chicago: Chicago Univ. Press, 2007, pp. 150–162.

Papanyan, S.B., To the ecology of the midday gerbil (*Meriones meridianus* Dahl.) in the Armenian SSR, *Biol. Zh. Arm.*, 1966, vol. 19, no. 5, pp. 68–80.

Papanyan, S.B., To the ecology of the Vinogradov’s gerbil in the Armenian SSR, *Biol. Zh. Arm.*, 1973, vol. 26, no. 4, pp. 65–73.

Patric, E.F., Reproductive characteristics of red-backed mouse during years of different population densities, *J. Mammal.*, 1962, vol. 43, pp. 200–205.

Pokrovsky, A.V. and Makarenets, I.A., Experimental data on breeding, reproduction, and hybridization of Eurasian *Lemmus* species, in *Gryzuny: materialy V Vsesoiuznogo soveshchaniya* (Rodents: Proceedings of V All-Union Conference), Moscow: Nauka, 1980, pp. 259–260.

Prokop’ev, N.P. and Vinokurov, V.N., *Uzkochechepnaya polevka v Tsentral’noi Yakutii* (*Microtus gregalis* in the Central Yakutia), Yakutsk: Yakut. Fil. Sib. Otd. Akad. Nauk SSSR, 1986.

Prokopov, K.P., Materials to the Ecology of the Eversmann hamster in the Zaisan Valley, in *Gryzuny: materialy V Vsesoiuznogo soveshchaniya* (Rodents: Proceedings of V All-Union Conference), Moscow: Nauka, 1980, pp. 260–261.

Rall, Yu. M., Introduction to the ecology of the midday gerbil *Pallasimys meridianus* Pall. II. Reproduction, *Vestn. Mikrobiol. Epidemiol. Paraziol.*, 1940, vol. 18, nos. 1–2, pp. 139–167.

Rall, Yu. M., To the ecology of the tamarisk gerbil *Meriones tamariscinus*, *Gryzuny Bor’ba Nimi*, 1941, no. 1, pp. 179–207.

Ramazanov, Kh.M., To the ecology of the field mouse in the Dagestan, in *IV S’ezd Vsesoiuznogo teriologicheskogo obshchestva: tezisy dokladov* (IV Conference of the Theriological Society of the USSR, Abstracts of Papers), Moscow: Inst. Evol. Morfol. Ekol. Zhivotn., 1986, vol. 1, p. 328.

Rylnikov, V.A., *Seraya krysa* (The Norway Rat), Moscow: Inst. Pestmenedzhmenta, 2010.
Samosh, V.M., Data on reproduction and fertility of the common hamster (Cricetus cricetus), Ekologiya, 1975, no. 5, pp. 97–98.

Shevchenko, V.L., Reproduction and a change in numbers of the steppe lemming (Lagurus lagurus) in the Urals region, Zool. Zh., 1963, vol. 42, no. 1, pp. 114–125.

Shvetsov, Yu.G., To the ecology of the root vole in the basin of the Selenga River, Fauna Ekol. Gryzunov, 1970, no. 9, pp. 218–230.

Shubin, I.G., The effect of population density on reproduction of some rodent species (Rodentia) in the steppe and semi-arid zones of Kazakhstan, Teriologiya (Theriology), Moscow: Nauka, 1974, vol. 2, pp. 271–280.

Sokal, R.R. and Rohlf, F.J., Biometry. The Principles and Practice of Statistics in Biological Research, New York: W. H. Freeman and Co., 1995, 3rd ed.

Sokolov, V.E., Sistematika mlekopitaiushchikh. Otriady: zaitseobraznykh, gryzunov (Systematics of Mammals. Orders Lagomorpha, Rodentia), Moscow: Vysshaya Shkola, 1977.

Sokolov, V.E., Isaev, S.I., and Pavlova, E.Yu., Some features of sexual maturation and reproduction of the great gerbil Rhombomys opimus under experimental conditions, Zool. Zh., 1983, vol. 62, no. 3, pp. 418–424.

Solomon, N.G., A reexamination of factors influencing philopatry in rodents, J. Mammal., 2003, vol. 84, pp. 1182–1197.

Solomon, N.G. and Keane, B., Reproductive strategies in female rodents, in Rodent Societies—An Ecological and Evolutionary Perspective, Wolff, J.O. and Sherman, P.W., Eds., Chicago: Chicago Univ. Press, 2007, pp. 42–56.

Tupikova, N.V. and Shvetsov, Yu.G., Reproduction of the water vole in the basin of the Volga and Akhtuba rivers, Vopr. Ekol., 1957, vol. 2, pp. 174–181.

Valentine, G.L. and Kirkpatrick, R.L., Seasonal changes in reproductive and related organs in the pine vole, Microtus pinetorum, in South Western Virginia, J. Mammal., 1970, vol. 51, pp. 553–560.

Wolff, J.O., More on juvenile dispersal in mammals, Oikos, 1994, vol. 71, pp. 349–352.

Wolff, J.O. and Lidicker, W.Z., Jr., Population ecology of the taiga vole, Microtus xanthognathus, in interior Alaska, Can. J. Zool., 1980, vol. 58, pp. 1800–1820.

Wolff, J.O. and Sherman, P.W., Rodent societies as model systems, in Eds., Rodent Societies: An Ecological and Evolutionary Perspective, Wolff, J.O. and Sherman, P.W., Chicago: Chicago Univ. Press, 2007, pp. 3–7.

Yakimenko, L.V., On the geographic variability of fecundity of the mole vole Eilemias talmius sensu lato, in Mlekopitaiushchie kak komponent aridnykh ekosistem (resursy, fauna, ekologiya, meditsinskoe znachenie i okhrana): tezisy mezhunarodnogo soveshchaniya (International Conference “Mammals as a Part of Arid Ecosystems (Resources, Fauna, Ecology, Medical Value, and Conservation,” Abstracts of Papers), Saratov: Inst. Probl. Ekol. Evol. im. A.N. Severtsova Ross. Akad. Nauk, 2004, pp. 166–167.

Zorenko, T.A. and Yakobsone, G.Kh., Peculiarities of development of the Brandt’s vole (Lasiopodomy brandti) during postnatal ontogenesis, in Okhrana, ekologiia i etologija zhivotnykh (Conservation, Ecology, and Ethology of Animals), Riga: Latv. Gos. Univ. im. P. Stuchki, 1986. pp. 25–44.

Zorenko, T.A., Golenishchev, F.N., and Skinderskaya, I.A., The features of behaviour of social voles of subgenus Sumeriomy (Arvicolinae, Microtus) under hybridization, Balt. Zh. Lab. Anim. Zhivotn., 1997, vol. 7, no. 2, pp. 77–102.

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