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Reproductive Characteristics of the Zokors (*Myospalax*, Rodentia, Spalacidae) in Eastern Russia

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Abstract—Original data on the dates of rutting, the birth of pups, the dispersal of the young, and the brood size of zokors, *Myospalax aspalax* and *M. armandii* in Transbaikalia and *M. psilurus* in both Transbaikalia and Primorskii krai, are presented. The available literature data on the reproduction of the members of the subfamily Myospalacinae from China, Russia, and Kazakhstan are analyzed and compared with data on the Myospalacinae from eastern Russia. The lowest fertility is shown to be characteristic of *M. armandii* in Transbaikalia and a generally low fertility of all species from eastern Russia in comparison with *M. myospalax* distributed in western Siberia. Many features such as a small brood size (from 1.75 in *M. armandii* to 4.67 in *M. myospalax* in Kazakhstan), the seasonal spring reproduction once a year, a solitary lifestyle even during rutting, long duration of the breeding season and of the dispersal of the young, and the predominance of females among adults are characteristic of all study species of both genera of the family, *Myospalax* and *Eospalax*.

Keywords: zokors, *Myospalax aspalax*, *Myospalax armandii*, *Myospalax psilurus*, breeding, Transbaikalia, Primorskii krai

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Zokors Myospalacinae Lilljeborg, 1866 are a group of highly specialized subterranean rodents of East Asia. The phylogeny and systematics of the group are controversial (Puzachenko et al., 2014; Zhang et al., 2022; Liu et al., 2022). Based on molecular genetic markers, modern zokors are considered to be part of the mole rat family Spalacidae as the subfamily Myospalacinae (Norris et al., 2004), represented either by one genus (*Myospalax*) or two genera (*Myospalax* and *Eospalax*).

The subfamily recognizes from five to 11 species (Wilson and Reader, 2005; Norris, 2017), of which five are in Russia (Pavlinov, 2012). The main part of the range of these species, except for the Altai zokor (*M. myospalax* Laxmann, 1733), lies within the territory of China and Mongolia (Zhang et al., 1997; Smith and Xie, 2013; Norris, 2017). When comparing the biological and ecological characteristics of different zokor species, we followed the currently prevailing views based on both morphological and genetic data. According to these data, among modern representatives of the genus *Eospalax* Seven species are distinguished, including the recently discovered *E. muliensis* sp. n. in the Sichuan Alps (Zhang et al., 2022), and in the genus *Myospalax,* there are four to five species (Puzachenko et al., 2009).

The biology and ecology of zokors remain poorly understood. The main studies were carried out for species living in the mountainous regions of China and concerned mainly various aspects of burrowing activity (Wang and Fan, 1987; Wang et al., 2000b; Zhang et al., 2003; Zhang and Liu, 2003; Fu et al., 2018) and nutrition and influence on vegetation (Wang et al., 2000a; Wang et al., 2008; Xie et al., 2014). Information on the reproductive behavior and breeding characteristics, such as timing of mating, rutting, pregnancy, lactation, and litter size, is very limited (Zheng, 1980; Zhou and Dou, 1990; Zhang, 2007). Of the species living in Russia, the most complete information on reproduction has been published for the Altai zokor, a significant portion of which was collected in Kazakhstan (Makhmutov et al., 1973; Makhmutov, 1978).

In Russia, in addition to the Altai zokor, which inhabits southwestern Siberia and northeastern Kazakhstan, representatives of the genus live in the southeastern part of Transbaikalia and in the south of Primorskii krai (Primorye). The daurian zokor (*M. aspalax* (Pallas, 1776)) is widespread in the Onon

River basin in Transbaikalia (Russia) and in Eastern Khentii and Eastern Khangai (Mongolia) (Bazhenov and Pavlenko, 2020). The Manchurian zokor (*M. psilurus* Milne-Edwards 1874) in the broad interpretation of this species is distributed from southeastern Transbaikalia through northeastern China to the western regions of Primorye, and to the south to the lower reaches of the Yellow River (Zhang et al., 1997; Puzachenko et al., 2009; Smith and Xie, 2013; Puzachenko et al., 2014). Representatives of *M. psilurus* from Transbaikalia and Primorye are considered as subspecies or independent species (Pavlinov, 2012; Puzachenko et al., 2014; Pavlenko et al., 2014, 2014a). The Armand zokor (*M. armandii* (Milne-Edwards, 1867)) is close to the Daurian, but a well-isolated morphologically and genetically species (Puzachenko et al., 2009), distributed in China from the middle reaches of the Yellow River in the south, up to the right tributaries of the Amur River in the north, the edge of the range enters Russia in the Transbaikalia along Klichkinskii ridge and presumably into Mongolia along the foothills of the Greater Khingan. In the reference book *Distribution of Mammalian Species in China 1997* (Zhang et al., 1997) the area of the supposed distribution of Armand's zokor is attributed to the range of the Daurian zokor. In the latest edition of the Red Book of the People's Republic of China, Armand's zokor is also listed as a synonym of the Daurian zokor (*China's Red List...,* 2021).

The known data on the reproductive biology of the Manchurian zokor in Primorskii krai were obtained on the basis of studying individual specimens (Kostenko, 1970). Information on the litter size and encounters with pregnant and lactating animals is limited, and information on mating times and gestation duration is virtually nonexistent. It is difficult to collect this data now, after the coastal population of the Manchurian zokor has been included in the Red Data Book of the Russian Federation (since 2001), since it requires the removal of a representative sample from the wild, so any new information is of particular importance.

Earlier, Kostenko (1970, 2000) noted that his materials confirm the data of Plater-Plokhotsky (1936) on the reproduction of the zokor in Primorskii krai only once a year, in April. According to Kostenko (1970, 2000), the number of young in a litter (based on an examination of six adult females) is 2–4, with an average of 3.1; by the first of May, the young reach a length of 10–12 cm. The lactation period continues until the first of June. Our observations allow us to supplement and clarify this data. In this article, we present results indicating the presumably low reproductive potential of this species.

Fragmentary information about the lifestyle, including data on reproduction, of the Daurian zokor in Transbaikalia was provided by Nekipelov (1946), and for Mongolia, by Skalon (1946). In the third ten days of June, N.V. Nekipelov caught two young of the year, each 14 cm long, and on June 6th V.N. Skalon captured suckling females. For the size of the brood of the Daurian zokor, N.V. Nekipelov based his estimation on information from hunters (four cases and in each case six pups were found). This information was apparently false, since, according to our data, the average litter size was 3.38, with a maximum of five pups. Subsequently, until the beginning of our research, no attention was paid to issues related to the reproduction of this species.

Data on reproduction in *M. psilurus* from Transbaikalia are even more scarce (Skalon and Nekipelov, 1936). Published data on the reproductive biology of *M. armandii* are absent.

The aim of our work is to generalize and analyze the materials obtained during expeditionary work to study the Manchurian zokor in the southwestern regions of Primorskii krai (Prikhankayskaya Plain) and in southeastern Transbaikalia, the Daurian zokor in southern Transbaikalia, and Armand's zokor in southeastern Transbaikalia. We compared the obtained results with the available published data on the reproductive biology of zokors.

MATERIALS AND METHODS

This work is based on field studies of zokors in the southern part of Primorskii krai for the years 1998–2007 and in southern and southeastern Transbaikalia for the years 1999–2023. The areas of work and localities were indicated previously (Pavlenko et al., 2014, 2014a; Bazhenov and Pavlenko, 2020). The names of districts in Primorskii and Zabaikalskii krais are given before some of them were transformed into municipal districts. Populations of the Manchurian zokor, in both the Primorskii and Zabaikalskii krais, are included in the regional Red Books. In addition, the Manchurian zokor of southern Primorskii krai is included in the new edition of the Red Book of Russia under the name Khanka zokor (*Myospalax epsilanus* Thomas, 1912) (*Red Book...,* 2021). In this regard, during the years of conducting research, the authors received permits from regional Ministries of Natural Resources to harvest a limited number of individuals and to conduct work on a census of small mammals, including zokor species.

Data on 341 captured zokor individuals were analyzed: 113 *M. psilurus* (*M. epsilanus*) from Primorye, and 73 *M. psilurus*, 118 *M. aspalax* (excluding newborn pups and recaptures), and 37 *M. armandii* from Transbaikalia. Of these, 113 individuals of *M. psilurus* from Primorye and 40 *M. psilurus*, 59 *M. aspalax*, and 25 *M. armandii* from Transbaikalia were dissected.

At the initial stages of this study, most of the captured zokors were subjected to standard zoological measurements and dissection. Skulls were collected, samples of genetic material were taken, and chromo-

Table 1. Brood size in different species of zokors

View	Research area	Brood size		Sample size (*n*)	Data source
		limits	average		
Myospalax aspalax	Transbaikalia	2–5	3.38 ± 0.28	13	Our data
Myospalax armandii	Transbaikalia	1–3	1.75 ± 0.34	8	Our data
Myospalax psilurus	Transbaikalia	1–3	2.50 ± 0.37	6	Our data
	Primorskii krai	1–6 (usually 2–4)	2.79	44	Our data;
		2–4	3.1	6	Kostenko, 1970, 2000
Myospalax myospalax	Southern Altai, Western Tarbagatai	1–10 (usually 3–6)	4.67 ± 0.08	618	Makhmutov et al., 1973
	Tomsk Oblast	1–8 (usually 3–6)	4.45 ± 0.21	66	Shubin and Erdakov, 1967
Eospalax baileyi	Tibetan Plateau, China	1–6 (usually 2–3)	2.75 ± 0.05	282	Zheng, 1980;
		1–6	3.19 ± 0.12	101	Wang and Li, 1993
Eospalax cansus	Tibetan Plateau, China	1–5	2.59 ± 0.14	57	Li et al., 1992; Wang and Li, 1993

some preparations were prepared (Puzachenko et al., 2009; Tsvirka et al., 2011; Pavlenko et al., 2014; Puzachenko et al., 2014). It was at this stage that it was possible to find out that within the supposed range of the Manchurian zokor in Transbaikalia, there are actually two species—the Manchurian zokor itself and Armand's zokor (*M. armandii* Milne-Edwards, 1867) (Korablyov and Pavlenko, 2007; Puzachenko et al., 2009), distributed parapatrically (Bazhenov and Pavlenko, 2020). Subsequently, taking into account the conservation status of zokors, the majority of the animals were released in the same place where the animal was caught after visual inspection, photographing, measuring the body weight and length, determining sex, and taking material for genetic research (Bazhenov and Pavlenko, 2020). Participation in reproduction for females and the expected size of the litters were determined in the standard way based on the number of placental spots in the uterine horns; the number of breeding, pregnant, and lactating animals, and the periods of observation of animals in the corresponding condition were taken into account. For males, the size and condition of the testes were recorded.

The ecology of the Daurian zokor was studied in more detail. In addition to capturing a small number of individuals in different parts of the range, long-term studies were conducted within the Tsasucheiskii island pine forest on the right bank of the Onon River in Transbaikalia (Ononskii district of Zabaykalskii krai). In particular, in the spring of 2011 and 2013, as complete a catch as possible was carried out, over several days in a row, on limited areas of several hectares with mapping of the burrows of individuals. (Sometimes it was not possible to catch one or two animals, but their presence and location were determined by fresh soil emissions in the opened burrow). In the first years of work (before 2011), capture was carried out with removal; in subsequent years, Daurian zokors were kept after capture, if necessary, for 2–3 days and then released back. It was attempted to keep in captivity several individuals of the Daurian zokor, including the following: four individuals were transferred to the Chita Municipal Zoo, where the animals, unfortunately, died within three months. To determine the timing of birth and monitor the development of the pups, in 2016–2017, in late April–early May, six female zokors were captured that showed no signs of nursing their pups and were kept in captivity for 1–1.5 months, after which they were released at the place of capture.

RESULTS AND DISCUSSION

Manchurian zokor (Primorye)

In Primorsky krai, 113 individuals of *M. psilurus* were caught in different years: 72 females, 40 males, and the sex of one animal has not been determined. Summarized data on the characteristics of the reproduction parameters are presented in Table 1.

Of the 72 females examined by us during the entire observation period, 44 (61%) participated in reproduction, 25 (35%) were determined to be nulliparous, of which 13 were subadults, and there was no data on reproduction for three animals. The proportion of ejaculated females was 21%. The number of placental spots varied from one to six. Most often females had two spots (38%), three and four spots were noted, respectively, in 22 and 25% of cases. The maximum number of spots, five and six, was noted once each. Cases of embryo resorption were recorded twice (in April–May). In one case, a lithopedion, a fossilized embryo, was found in a female who had just given birth (village of Ilyichevka, Oktyabrskii district of Primorskii krai, end of October). The average number of pups per female that had given birth, based on the number of placental spots, is 2.79, i.e., slightly lower than previously estimated at 3.1. Pregnant and lactating

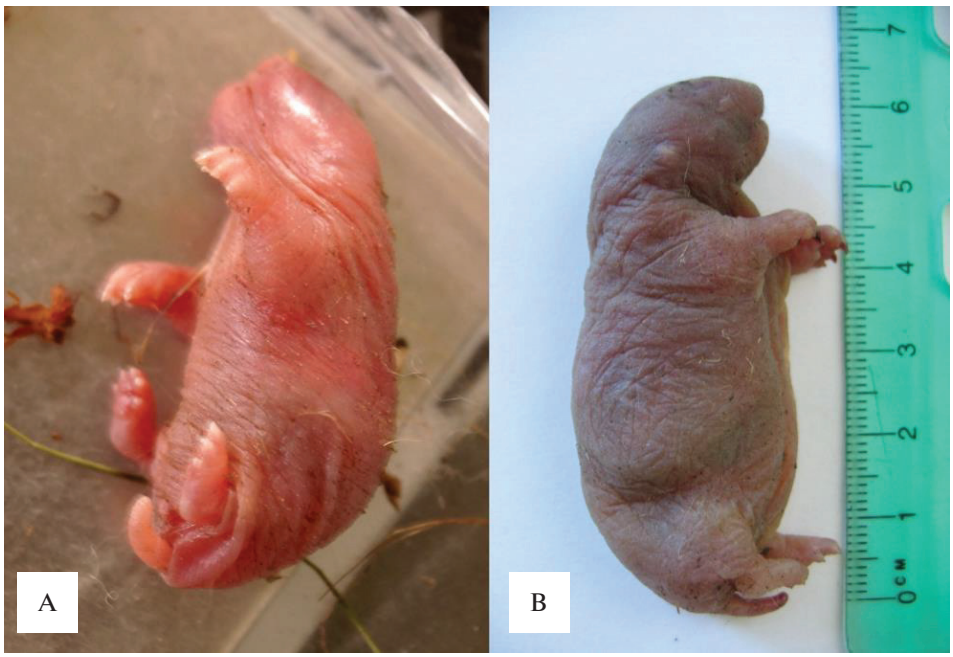

Fig. 1. Newborn zokors: (a) Daurian and (b) Manchurian from Primorskii krai. Photos by the authors.

females were encountered both at the end of April and at the end of May and the first half of June. The first lactating females were encountered at the end of April. In the last days of May, females with almost mature embryos were noted, in one case with four embryos up to 40 mm in length (Gladkaya Pad, Pogranichnyi District, end of April), as well as females in the early stages of pregnancy. The last pregnant female was noted by us on June 15 (Karantinnaya Pad, Primorskii krai, Pogranichnyi district). The next day after capture, the female gave birth to one pup, which died on the way to the vivarium and was not carefully examined or photographed by us.

The only newborn pup that we were able to examine carefully, describe, and photograph was born on May 29–30 to a female captured the day before in Priluki (Primorskii krai, Khorolskii district). It had external characteristics similar to those of the newborn Altai zokor (Makhmutov et al., 1973): the body length was 64 mm, the skin was pink, wrinkled, there was no fur, the eyes were closed, the front and back paws had small developed claws on the fingers (Fig. 1b). Kostenko (1970) reported the last sighting of a lactating female on June 7.

There were two reliably documented cases of more than one animal being caught in one burrow at the end of May in Pad Gladkaya (Primorskii krai, Pogranichnyi district). In one burrow, two young animals were caught together with an adult female who had just given birth (three placental spots), presumably their mother. Both turned out to be males, reaching 180 mm in length and with testicles measuring 5.8 × 4.2 mm, 6.3 × 4.8 mm. Placed together in the same cage, the animals behaved in a friendly manner. In the same locality, but in another part of a vast ravine, at the end of May, an adult pregnant female (two placental spots in one horn, one embryo in the other) and a young male (body length 197 mm, testicle size 8.5 × 5.8 mm) were caught from the same hole.

We did not observe mating. Placed together, the animals of different sexes were extremely aggressive towards each other. Attempts to place animals of different sexes from the same locality in the same terrarium, even in the spring, usually ended with the expulsion of the male.

Whether mating occurs in the fall remains a question. We have no direct evidence that mating occurred in the fall; the latent phase of pregnancy was noted at the time of examination of the female. However, data from autopsies of females in autumn allow us to assume that processes of activation of the reproductive state of females are underway. Thus, in a number of cases we have noted swelling (intumescence) of the uterine horns in the autumn period, in October, in both females that had given birth and females that had not given birth, and even a significant development of the uterine blood supply system in one of the females. Our data rather indicate spring reproduction. Thus, three carcasses of zokors from the nest of an eagle owl, collected on April 29, 2006, in the Oktyabrskii district of Primorskii krai in the valley of the Talovka River, were examined (material received from ornithologists V.N. Kurinnyi, S.G. Surmach, and I.V. Donchenko). Judging by the condition of their internal organs, the

Fig. 2. A small Manchurian zokor, caught in a burrow next to the burrow of an adult female (pictured) in early May in Transbaikalia. Photos by the authors.

animals were healthy, well-fed, with a well-developed layer of subcutaneous fat. All three zokors turned out to be sexually mature males with well-developed testes, and the testes of one of them turned out to be the largest compared to the testes of all the animals we examined (13 × 9 mm). The fact that the eagle owl hunts indicates that the zokors come to the surface at twilight and at night. Based on the timing of the hunt and the state of the reproductive system, it can be assumed that the animals were moving in search of females.

The duration of pregnancy is apparently at least a month. Thus, one of the females, captured on April 27 near the village of Krounovka (Ussurii district), was placed in a terrarium for observation. The female exhibited well-defined nesting behavior, had developed mammary glands with swollen nipples, and a rounded, thick belly. However, the birth did not take place. At autopsy on June 6, after the behavior of the animal had changed, two placental spots were found in one horn (presumably from a previous birth) and traces of resorption of two embryos in the other.

Manchurian zokor (Transbaikalia)

The timing of the rutting and pregnancy of the Manchurian zokor in Transbaikalia remains unclear. The appearance of fresh soil emissions in the spring among the Manchurian zokor in Transbaikalia occurs later than in Primorye and later than among the Daurian zokor in Transbaikalia. The most active occurrence of soil ejections is observed from the first days of May (for the Daurian, almost a month earlier). Most likely, the late peak of burrowing activity is due to the fact that the soil in the habitats of the Manchurian zokor is more clayey and more humid and therefore thaws later than the sandy and sandy loam soil in which the Daurian zokor most often builds burrows. Presumably, rut for this species in Transbaikalia occurs at a later date than for the Daurian. Among the nine individuals caught in early May were four females, four males, and one very small specimen weighing only 110 g (Fig. 2) (all animals were released). No lactating females were observed. The small animal was caught in its own separate burrow (with a passage diameter corresponding to its size), located next to the burrow of a large adult female. On this basis, we assume that these were a female and her pup of the previous year (with an extremely low body weight; a similar case is known for the Daurian zokor). Of the three females caught between June 14 and 21, no pregnant ones were noted; two had dark spots, and the third had not previously participated in reproduction. At the same time, Skalon and Nekipelov (1936) reported the discovery on July 9 of a female with two well-developed embryos.

According to our data on the number of placental spots, the size of the brood of *M. psilurus* in Transbaikalia ranges from one to three, with an average of 2.50 ± 0.37 pups ($n = 6$). Manchurian zokors from Primorye and Transbaikalia do not differ statistically in brood size.

Daurian zokor

There is no reliable information in the literature about the mating season of the Daurian zokor. Nekipelov (1946), citing hunters, reported that in April and early May it was sometimes possible to catch zokors not only singly, but also in pairs, and some females "have their fur pulled out on their rear ends." Our data confirm that maiting occurs in the spring during the period of the beginning of active digging activity. In Transbaikalia, the earliest appearance of fresh soil emissions was noted at the end of March–beginning of April, and mass emissions, from mid-April. The second half of April marks the peak of zokor digging activity, when the greatest amount of soil ejecta occurs. In May, new soil ejections appear less frequently, and in the summer the animals usually redistribute the soil along previously dug passages. The peak of fresh soil emissions in autumn (September–early October) is much smaller than in spring. The autumn peak of activity is associated with the preparation of the winter burrow and increased storage of food (Nekipelov, 1946; Bazhenov, 2016), and the spring peak, apparently, is mainly associated with reproduction (search for a sexual partner). The longest, often almost straight, fresh spring passages belonged to males. The spring mating season is evidenced by fragmentary data showing a gradual involution of the testes and their appendages in males from April to November, so there is no reason to assume the presence of autumn mating in the Daurian zokor. The length of the testes of adult males (excluding young of the year) in April was 9 mm ($n = 4$); in May, 7–9 ($n = 3$); in June, 7–9 mm ($n = 4$); in August, 7–8 mm ($n = 2$); and in September, 7–8 mm ($n = 2$). The maximum development of the epididymis was observed in April, then (by autumn) a gradual involution occurred.

We did not note any connections between the surface passages of individuals living in close proximity. But in April, 30- to 50-centimeter sections of soil were found, connecting the burrow systems of neighboring animals, which was not observed at other times of the year. In one case, it was a male and a female; in the second case, it was a female and an animal of unknown sex (based on the diameter of the burrow, presumably a male). In April, after the capture of males, no one visited their burrows for 1–2 days; after the capture of females, it was sometimes possible to find traces of visits by other zokors (presumably males). In one case, a female was caught first, and half an hour later, a male was caught in the same hole. Also in mid-April, a very large male with developed testicles was observed emerging to the surface and making an unsuccessful attempt to create a new burrow: the animal ran into a layer of frozen ground, died, and was discovered during the excavation of this new burrow. This is the only reliably recorded case of an adult Daurian zokor coming to the surface in the spring–summer period of the year. Typically, only young of the year are found on the surface from mid-summer to mid-autumn. Presumably, the adult male left his previous burrow in search of a female.

The earliest case of capturing a pregnant female Daurian zokor was recorded on April 20 (the embryos were about 10 mm in diameter). But it should be noted that we usually did not catch zokors before April 15th. The latest cases of capture of pregnant females were May 14 and 25 (fully formed embryos about 25 mm long). Nursing females were usually found in June–July, and only one on May 1. Thus, according to the available data, the birth of Daurian zokor pups occurs from the end of April to the end of May.

During temporary captivity of six adult female Daurian zokors, captured at the end of April–first days of May and not nursing at the time of capture, the birth of pups was observed in two cases. One of the females gave birth to a single pup weighing 10.1 g on May 9 (Fig. 1a). There is no certainty that this was the only pup in the brood, since they tried not to disturb the female for two days after the birth of the first pup, but, apparently, she ate her brood. In the second case, the female gave birth to three pups on May 5th. Although this female showed some care for her offspring, the newborns did not survive and died within two days.

We do not have precise information about the duration of pregnancy in this species, but judging by the fact that the last cases of mating occur around April 20, and the birth of pups occurs at the end of May (or even the first days of June), the duration of pregnancy is presumably 30–40 days. The timing of rut is thus limited to the period from the end of March to the end of April; i.e., it coincides with the period of the beginning and peak of active digging activity.

Of the 27 dissected adult (wintered) females, 18 (67%) participated in reproduction in the current year. We have information on the number of embryos in four Daurian zokor females, the number of placental spots in another eight, and the total number of newborns in one female. The litter size, calculated based on all three indicators (number of embryos, number of placental spots, number of newborns), was 2–5, with an average of 3.38 ± 0.28 ($n = 13$). We also have information on the number of grown-up pups before their dispersal began in early July, based on the complete capture of animals in four burrows: 1–3, on average, 2.0 ± 0.5 animals.

The dimensions (mm) of three newborn Daurian zokor pups from one litter, each weighing 9.5–9.6 g, were body length 52–56, tail length 10.6–11.4, foot length 8.3–9.0. The weight of the only pup, born to another female, was 10.1 g. The pink, folded skin was hairless, the muzzle had white whiskers about 2 mm long, the toes were not separated, the claws were gray–pink, and the length of the largest claw on the front paw was 2.3 mm. The eyes and ear canals are closed (Fig. 1a).

The postnatal development of Daurian zokor pups has not been studied. We can only judge the growth rate based on a few catches of young individuals. At the end of June and the beginning of July, the body weight of young of the year of both sexes, caught in maternal burrows, was 90–140 g ($n = 8$) with a body length of 14–16 cm. In September–October, the body weight reached 130–170 g with a length of 16–17 cm. At the beginning of April, an adult animal (female) was caught, which survived the winter, despite its extremely small size (body weight 120 g, body length 153 mm).

The first cases of young appearing on the surface were recorded in the last days of June (the remains of the young were noted under the nest and in the pellets of the long-eared owl). Most likely, during this period the animals have not yet moved out of their mother's burrow, but feed on green parts of plants at the very surface of the soil. During this time, we often observed narrow ridges of soil raised above the surface, in which plant stems with bitten-off underground parts remained. Reliable cases (results of capture in zoological trenches) of dispersal of pups (body length 145–150 mm and body weight 100–120 g) on the surface were recorded starting from the end of July. The resettlement period is very extended. For example, on September 18, a young of the year with a body length of 168 mm and a weight of 172 g was caught on the surface. In another case, young of the year was caught on September 25 from a narrow burrow connected to a wider burrow of an adult female. In April and early May, during intensive excavations of burrows in the passages of females, pups born the previous year were not observed even once.

Among the adult Daurian zokors, we captured during the entire study period, including animals whose sex was determined during life, females predominate in a ratio of 1 : 1.39 ($n = 91$), and only in animals the sex of which was confirmed at autopsy, is the ratio close at 1 : 1.56 ($n = 41$). In young of the year ($n = 20$), which were caught in the period from June 30 to November 18 and the sex of which was taken into account only based on the results of autopsy, the sex ratio was 1 : 1.

Armand's zokor

Armand's zokor remains the least studied species of the genus *Myospalax* in the Russian Federation. We do not have data on Armand's zokor for the spring period. Among the four females caught in the third ten days of June, two were pregnant, one showed signs of a recent pregnancy, and one (the smallest in size, probably a young of the year) had not participated in reproduction. Despite the fragmentary nature of the information, differences in the timing of reproduction in *M. armandii* and *M. aspalax* in Transbaikalia are obvious. In *M. aspalax* in June, only lactating or nonbreeding females were noted, and for *M. armandii* at the end of June, two of the three females had not yet given birth. We have information on the number of placental spots and the number of embryos in eight female Armand's zokor from Transbaikalia over different years. Their number ranged from 1 to 3, with an average of 1.75 ± 0.34 ($n = 8$). Among the captured adult specimens, females predominate statistically insignificantly in the ratio 1 : 1.5 ($n = 30$). Among the individuals under one year old, four males and five females were caught.

The proportion of females participating in reproduction in the zokors of the genus *Myospalax* was not high. In Tomsk oblast, 16% of females *M. myospalax* were unfertile (Shubin and Erdakov, 1967). In Kazakhstan, on Ubinskii Ridge, the percentage of unfertilized females of the same species is 8.3–8.4% (Makhmutov, 1978). According to our data, 21% of wintered females of *M. psilurus* from Primorye and 33% of *M. aspalax* from Transbaikalia had not participated in reproduction. One of the main reasons for this phenomenon in general is the difficulty of contacts between individuals of different sexes in an exclusively underground lifestyle, especially at low population density. Makhmutov (1978) from the example of *M. myospalax* showed that among overwintered females, the largest proportion of individuals not participating in reproduction falls in the smallest weight group, which apparently consists mainly of individuals of the previous year. According to our data, Daurian zokor females that participated in reproduction are not significantly larger in weight and body length than those that did not breed (247 and 226 g, 185 and 180 mm, respectively). Apparently, females that have overwintered for the first time participate in reproduction to a lesser extent: among females that have given birth and/or are nursing, individuals with small body sizes (165–170 mm) and weights (from 180–190 g) were noted.

There is little information about the behavior of zokors during rut. According to the results of radio tracking, mating *E. baileyi* from the Tibetan Plateau occurs in a temporary tunnel connecting the burrows of animals of different sexes (Zhou and Dou, 1990). To achieve this, during the mating season, males dig long tunnels, which increases the chances of meeting females (Zhang, 2007; Zhou et al., 2022). A solitary lifestyle and larger home ranges in males are characteristic of species with a promiscuous mating system (Gromov, 2008). Our observations show that the behavior of *M. aspalax* in Transbaikalia during rut is generally similar to that described in the literature for *E. baileyi*. During the spring peak of digging activity, Daurian zokor males dig very long, often straight, tunnels, apparently allowing them to locate the habitats of neighboring females more successfully. Encounters of two adult individuals in one burrow were noted only in April. According to our data, the period of birth of Daurian zokor pups in Transbaikalia begins in late April and continues until the end of May. The main

mating period is in April, but signs like thawing of the soil, observations of isolated traces of digging activity, and, most importantly, data on the birth of young in the last days of April indicate that mating probably begins at the end of March. We did not observe any signs of autumn rut during the field work period (up to and including mid-November). From November to March, the surface layers of the soil in Transbaikalia freeze, and the digging of new burrows to search for a sexual partner is unlikely unless such passages are prepared in the fall. The system of deep passages (below the level of soil freezing) in the Daurian zokor, according to published data, includes a nest and storage rooms connected to the surface by tunnels (Skalon, 1946; Nekipelov, 1946). Branched systems of deep passages capable of connecting the burrows of neighboring animals have not been discovered.

The prolongation of the mating season and the birth of pups is also characteristic of other representatives of subfamily Myospalacinae. So, pregnant *E. baileyi* females were caught from mid-April to mid-June (with a peak from the third ten-day period of April to the third ten-day period of May), and the period of birth of pups in this species is in the interval from mid-May (but mainly from the last ten-day period of May) to the first days of August (Zheng, 1980). Thus, pregnancy in *E. baileyi* is estimated to be 30 days or a little more, and the period when researchers note the birth of pups in the majority of females lasts 40 days. The gestation period for other zokor species is likely to be similar to that reported. We believe that the gestation period for the Daurian zokor is also about a month or a little more, and the mating season lasts at least a month.

Published data on the timing of rut of the Altai zokor's are uncertain and even contradictory. It has been suggested that this species has an autumn rut (Shubin and Erdakov, 1967). In the Altai zokor in Altai and Tarbagatai, birth ends by the end of March (Makhmutov, 1978), and in the northern part of the range, by the end of April (Shubin and Erdakov, 1967; Potapkina, 1970). For the southern part of the range, data are provided on the involution of testes from April to October and on the beginning of the activation of the reproductive gonads of males and females in November (Makhmutov et al., 1973). The onset of gonad activation in November does not indicate the beginning of the breeding season: the female follicles are far from maturing, and spermatogenesis was observed in only one case; the weight of the testes is more than two times lower than in April. Thus, the mating season for the Altai zokor in Kazakhstan falls in winter: it begins no earlier than December and ends no later than the end of February. If we reject the hypothesis of the presence of a latent phase in the development of embryos and accept the duration of pregnancy as approximately one month (as for *E. baileyi* and *M. aspalax*), then rut of the Altai species in the southern part of its range should take place in February or a little earlier, and in the north, in March.

Encounters of pregnant and lactating females between the end of April and mid-June, the absence of direct evidence of a latent phase of pregnancy, and an estimated gestation period of about a month all suggest that rut in *M. psilurus* in Primorskii krai most likely begins in March and lasts until mid-May. This is also indirectly supported by the appearance of active sexually mature males on the surface at the end of April during the dark hours of the day. The meeting of immature animals in the same burrow with a female at the end of May may indicate an earlier start to the mating season than March.

Based on fragmentary data on *M. psilurus* in Transbaikalia, the mating season for this species occurs approximately in May–early June; the pregnancy period is in May–early July, and the birth of the pups is in June–early July. The pups born latest (in July) are likely to be slow in growth and, in the spring of the following year, may have a body weight 2–3 times less than that of sexually mature adults. For *M. psilurus* in Primorskii krai, in a milder climate, these dates, as mentioned above, occur a month earlier. The timing of rut, pregnancy, and birth of Armand's zokor in Transbaikalia remains unclear.

The smallest brood size (1.75) was found in Armand's zokor (from Transbaikalia); it is reliably lower than in all other species for which information is available (Table 1). The Manchurian zokor from Transbaikalia has a relatively small brood size of 2.5, which is significantly lower than that of the Altai or Daurian zokor. The brood size of the Manchurian zokor (2.79) in Primorye is slightly larger than in Transbaikalia, but the difference is not significant.

The proportion of males among adult (wintered) individuals of almost all species of zokors (Table 2) is smaller than the proportion of females. This is likely a consequence of increased mortality from predators and other factors, which in turn is associated with more frequent and longer migrations of males across the soil surface. This assumption is supported by the aforementioned case, when a male emerged to the surface in early spring and attempted to migrate, but it all ended in his death, as well as cases of catching single males of this species, the settlements of which were removed from the nearest habitats of other zokors at a distance of several hundred meters to 1–2 km. Surface movements are also evidenced by the discovery in April of three carcasses of male Manchurian zokors in the nest of an eagle owl in Primorye. The literature provides another explanation for the low proportion of male zokors in the population. According to Zheng (1980), in *E. baileyi* embryos weighing more than 2 g, the proportion of males is less than the proportion of females 1 : 1.31 ($n = 275$), in adult animals this ratio is 1 : 1.52 (Table 2). It should be noted that, in this case, despite the sample size, the difference in the propor-

Table 2. Sex ratio of adults of different species of zokors

View	Research area	Number of females per male	Sample size (*n*)	Data source
M. aspalax	Transbaikalia	1.56 1.39	41 91	Our details: — based on autopsies only — including lifetime sex determination
M. armandii	Transbaikalia	1.50	30	Our data
	China*	1.14	122	Luo et al., 2000
M. psilurus	Transbaikalia	1.13	49	Our data
	Primorskii krai	1.80**	112	Our data
	China	1.13	117	Luo et al., 2000
M. myospalax	Tomsk oblast	1.86**	103	Shubin and Erdakov, 1967
	Northeast of Kazakhstan	1.53***	1219	Makhmutov et al., 1973
E. rufescens	Shanxi, China	0.93	29	Luo et al., 2000
E. rothschildi	Shanxi, China	1.70	62	Luo et al., 2000
E. baileyi	Tibetan Plateau, China	1.52*** 1.41***	1824 606	Zheng, 1980; Wang and Li, 1993
E. cansus	Gansu, China	2.18***	687	Wang and Li, 1993

* The source cites it as *M. aspalax*. ** The difference from an equal sex ratio is statistically significant according to the χ^2 method at $p = 0.05$. *** The same, at $p = 0.01$.

tion of males and females in embryos is statistically insignificant. In Kazakhstan in *M. myospalax* the predominance of females among young animals (up to one year) is insignificant and unreliable (1 : 1.09), and among adults, reliable (1 : 1.52) (Makhmutov et al., 1973). Thus, a slight sex imbalance in favor of females in zokors is possible even at birth, but increases in the postnatal period.

Newborn pups of the Daurian zokor (9.5–10.1 g) were inferior to larger species like the Altai zokor in weight (13.3 g) with a similar body length (52–56 mm) (Shubin and Erdakov, 1967), and the Manchurian zokor from Primorye in body length (64 mm) (our data). The newborn pups of the indicated species did not differ in the degree of embryonic development.

The rate of development of young animals of different species apparently differs. According to our data, young of the year of the Daurian zokor begin to disperse from the mother burrow at the end of July, when they are presumably 2–2.5 months old. It is possible that cases of catching very small young Daurian zokors in late autumn and spring are associated with periods of pregnancy and birth that were later than usual. According to Kostenko (1970), young Manchurian zokors live with the female in Primorye throughout the spring and first half of the summer. By October, when the body length is about 19 cm, the young of the year have their own burrows on the periphery of the mother burrow. The following spring, having reached sexual maturity, they disperse across the surface of the earth. Our observations do not refute, but also do not supplement the information published by V.A. Kostenko.

CONCLUSIONS

Zokors are characterized by low potential fertility. All species of zokors are characterized by reproduction once a year and small litter sizes from 1.75 (Armand's zokor) to 4.67 young (Altai zokor in Kazakhstan). The litter size of the Manchurian zokor is 2.79 in Primorye, 2.50 in Transbaikalia, and 3.38 for the Daurian zokor. All forms of zokors in eastern Russia are characterized by lower fertility than the Altai zokor in Western Siberia and Kazakhstan. Low fertility is a biological feature that makes zokor populations vulnerable to a sharp decline in numbers as a result of anthropogenic activity (habitat destruction, direct extermination). Along with the weak ability to disperse over long distances, which is associated with an underground lifestyle, low fertility under intensive anthropogenic impact leads to a reduction in the range and numbers of primarily peripheral populations of zokors.

Among adult zokors, in most studied species of both genera (except *E. rufescens*) a predominance of females is observed in populations, although for species in the eastern part of Russia these disproportions are statistically insignificant in small sample sizes. The breeding season is extended; rut occurs in the spring after the top layer of soil has thawed. Even during the mating season, the animals live solitary lives; contacts between individuals of different sexes are short-lived. In the search for a female, males dig long tunnels and probably sometimes make overground crossings on the soil surface. Young of the year often disperse along the soil surface; the dispersal period is very extended and depends on the species and region of habitat.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This work was carried out in accordance with the rules adopted by the European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes (1986) and Annex VIII of Directive 2010/63/EU of the European Parliament and of the Council of the European Union of September 22, 2010, on the protection of animals used for scientific purposes. The work program was approved by the Bioethics Commission of the Federal Scientific Center for Biodiversity of Terrestrial Biota of East Asia, Far East Branch, Russian Academy of Sciences (Protocol no. 4 dated February 16, 2024).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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