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Postembryonic Development of The Edible Dormouse (*Glis Glis* Linnaeus, 1766)

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Abstract

The period of postnatal development in the edible dormouse occurs before hibernation, causing a restricted period of growth. Four stages can be identified according to the morphological development and behavior in the nesting period. Dormice are born completely naked, unable to move independently. During the second stage (11–21 days), juveniles acquire a variety of movements. The third stage (22–30 days) begins with opening the eyes and is associated with the activity outside the nest. During the fourth stage (31–44 days) juveniles gradually become independent of their mother. Bright peculiarity of the species postembryonic development is three simultaneous ways of feeding from the 16th day up to the end of lactation on the 39-43rd days: milk, chewed by mother food and firm forages. In social interactions cases of strict aggression are scarce. Dynamic socio-hierarchical structure of litters with the absence of stepped hierarchy is observed. As a whole, during the period of early ontogenesis strategy of the species provides the maximal survival of posterity instead of concurrence inside litters. Geographical differences in time frames of early ontogenesis, found when comparison of data from different regions, maybe caused both by intraspecific variation and peculiarities of local populations.

Keywords: edible dormouse, Glis glis, postnatal development, early ontogenesis, juveniles, Zhiguli Mountains

1. Introduction

In the life cycle of mammals, the period of early ontogenesis is of key importance for the survival of young animals. In hibernating animals, the period of growth and accumulation of fat reserves by juveniles before hibernation is limited by strict time frames. Therefore, in the ontogeny of such species, some features can be traced that are critical for survival during the period of the first hibernation, when a significant proportion of young animals are eliminated.

Bright example in Europe is the edible dormouse (*Glis glis* Linnaeus, 1766) – nocturnal hibernating rodent with anomaly long life expectancy – up to 14 years (Morris 2004). The edible dormouse has one litter per year (Rossolimo et al. 2010, Kryštufek 2010). Peculiarity of reproductive cycle is reproduction skipping in separate years (Bieber 1998, Schlund et al. 2002, Pilastro et al. 2003, Ruf et al. 2005,

Vekhnik 2019). Number of juveniles varies from 1 to 12 juveniles in different countries, 6-7 are common (Spangenberg 1935, Özkan et al. 2002, Milazzo et al. 2003, Fietz et al. 2005, Pilāts et al 2009). Despite long history of research, the ontogeny of the dormouse is described in detail only in several monographs of last century: by von Vietinghoff-Riesch (1960), von Koenig (1960), Ayrapetyants (1983) and Lozan et al. (1990). Studies were conducted in several plots of Central Europe and Eastern Europe and in the Caucasus. In the most part of the species distribution range such observations were not conducted. The current research was conducted in the most eastern population of the Zhiguli Mountains (Russia). In peripheral populations local peculiarities could be found. Comparison of our data with the observations from other plots contribute to the review of the species early ontogenesis.
As geographic differences may have a place, data from other regions are given when any discrepancies are found in the timing of particular stages. When the terms coincide, data of other authors are not cited. Based on our own and literary data on the postembryonic growth, four stages were identified according to the features of behavior, caused by stages of morphological development.

2. Material and methods

Laboratory observations were conducted in 2005–2007 over three litters of 4, 6 and 7 juveniles. Female dormice at the last stage of pregnancy were caught in their natural habitat. After giving birth, each litter was observed daily from 0 to 8 hours for 45 days (until the end of lactation). Natural lighting was maintained in the laboratory; at night, weak LEDs, predominantly red, or a red lamp were used. Daytime observations were carried out periodically after the animals began to independently get out of the maternity nest and move freely around the nest boxes. In addition to the stages of physical development and the time of occurrence of behavioral reactions, various types of contacts were recorded. In total, about 1080 hours of observations of the edible dormouse ontogenesis were conducted and 1349 encounters were recorded between individuals in litters. At 48-50 days of age, all litters were released in the places of capture of pregnant females.

3. Results and discussion

In the study on the eastern periphery of the range in the Zhiguli Mts. body mass of juveniles varies from 2.4 to 4.6 g, the growth rate is about 1.3 g per day. The changes of body mass of juveniles in one of the litters of six juveniles in captivity are presented in the Figure. 1.

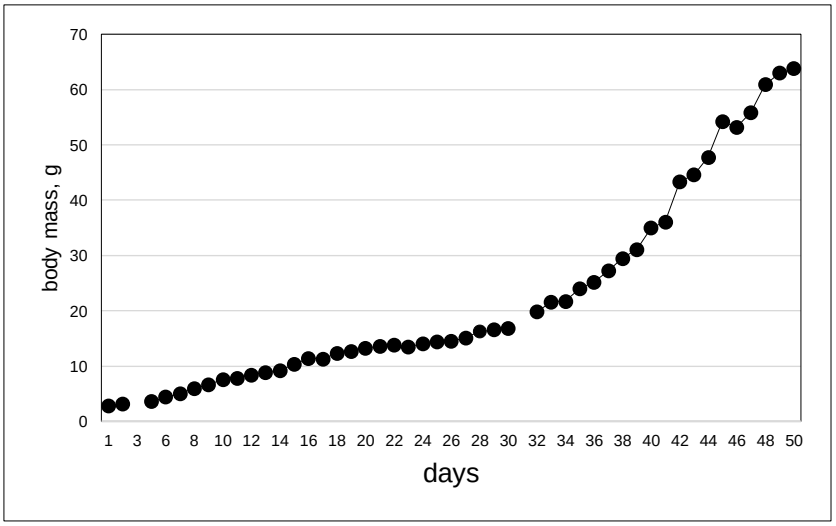

Figure. 1*. The growth rate of the edible dormouse (one of litters, 6 juveniles).*

Body mass and growth rate vary in different regions. Besides, litter size has a great influence on these parameters of juveniles. In the introduced population of England, the rate of growth sometimes achieves more than 1.5 g per day (Morris 2004). In Germany, the body mass of a newborn is about 2 g, the length

of the body averages 40 mm and of tail 20 mm, the growth rate is about 1.2 g per day (von Vietinghoff-Riesch 1960). In Austria mean body mass of juveniles is 3.7 ± 0.6 g. Mean weight gain per individual was 1.28 g per day within the first 30 days of life (Bieber and Ruf 2004). In Moldova and Ukraine body length is about 30–35 mm (Lozan et al. 1990). In the Caucasus (Russia) average body mass of a newborn is 2.5 g, the length of the body is 30 mm (Donaurov et al. 1938).

4. Stages Of Postembryonic Development

4.1 Neonates

Dormice are born completely naked; their blood vessels shine through their skin (Figure. 2). The head is greatly enlarged in comparison with adults. The fingers are fused, without claws. The eyes and ears are closed. Chaotic uncoordinated movements are observed. When crawling on a flat surface, dormice often fall on their back.

Figure. 2. New-born juveniles of the edible dormouse

In the behavioral repertoire in the first days of life, there are innate elements of feeding behavior: the reaction of search of a nipple and the sucking. During the lactation period, almost all the time while the mother is in the nest, all or some of the juveniles try to suck milk. No preferences were found when searching for nipples. There was no dominance of one or more small dormice during sucking. From the first day, the juveniles exhibit a crowding reaction. In the absence of the female, they crawl on top of each other, forming a dense ball. This tendency persists throughout the nesting period. A similar phenomenon is observed in adult non-relative animals during sleeping.

4.2 I stage (1–10th days)

Nestlings are completely dependent on their mother and are not able to perform most of the vital activities.

3rd day. The juveniles are able to maintain balance for several seconds – posture reflex.

5th day. The skin of the young mammals begins to obtain a grey tint due to the commencing fur growth (Figure. 3). According to von Koenig (1960), the auricles detach. Crawling becomes faster, but movements remain uncoordinated. Juveniles are able to climb over each other.

Figure. 3. Juvenile of the edible dormouse on the 4th day of life

7th day. Juveniles try to walk, but they often stumble and fall on their backs. On days 7–9, elements of comfort and play behavior appear in different litters. They push, creep on top of each other, butt.

According to Airapetyants and Fokin (1984), on the 6–7th days a species-specific defensive reaction appears, conventionally called "flinching". It manifests in the absence of the mother in the nest as a sharp start of disturbed nestlings and subsequent freezing.
8th day. Juveniles' limbs are noticeably lengthened and the toes on the paws begin to separate.
9th day. Color differentiation on the limbs begins: a grey stripe on the front surface of the tarsus and white color on the dorsal side become contrasting. The mammals begin to walk fairly confidently and stop rolling over on their backs. The grasping reflex is clearly manifested. According to Lozan et al. (1990), on the 8–10 days, juveniles are able to crawl over various small obstacles. When new sounding, smelling strongly or moving objects appear, juveniles show "flinching" and simple defensive acts.

4.3 II stage (11–21 days)
At the beginning of this stage, instead of the round-the-clock polyphasic activity, a monophasic diurnal rhythm with a night-active period is formed, which is characteristic of adults. The coordination of movements is improved; many new elements appear in the behavior.
11th day. According to von Koenig (1960), the fur becomes velvety. Comfort behavior is formed: dormice can clean the head and sides in lateral positions (von Koenig 1960). A negative light reaction arises. The movements acquire considerable complexity and variety.
12th day. Claws on the fingers become noticeable. The hairs on the back become distinguishable (Figure. 4). The tail is covered with separate hairs. The differentiation of coloration, which is now like the coloration of adults, is coming to the end. In place of the eyes, black slits become noticeable. According to von Vietinghoff-Riesch (1960), at this time the juveniles demonstrate strong defensive reactions with the help of punches by their paws and lay on their backs.

Figure. 4. Juveniles of the edible dormouse on the 12th day of life

13th day. The fingers are completely differentiated. Lower teeth appear. According to the observations of Airapetyants (1983) on the ontogeny of dormice inhabiting the Caucasus, as well as von Vietinghoff-Riesch (1960) in Germany, the differentiation of fingers and appearance of the lower incisors occur earlier, on the 10th day of life. According to Donaurov et al. (1938), the lower incisors appear already on the 7th day. On days 13–15, aggressive reactions are recorded inside a litter (relay aggression), as well as sudden sharp alternating shudders during sleeping. Similar elements of aggressive behaviour in dormice from the territory of Austria are formed on the day 10 (von Koenig 1960). Attempts to get out of the nest are recorded. According to von Koenig (1960), awkward running begins.
15th day. The hairs on the abdomen become distinguishable. According to Airapetyants (1983), at this age a defensive reaction appears in the nest during the absence of the mother: suddenly disturbed juveniles begin to simultaneously start rhythmically shuddering. According to Lozan et al. (1990), this occurs as early as day 12. Also, Lozan et al. (1990) and Airapetyants (1983) note that at the age of 15 days, juveniles are able to move by jumping and crawling on a vertical surface.
16th day. There is a transition of young dormice to a mixed diet: the female begins to feed the juveniles from the mouth with chewed dense food. In this case, the female can simultaneously feed one small dormouse through the mouth, while the rest suck milk. In behaviour, a begging reaction is formed, in which the juveniles touch their mother's face with their paws. There is a very intense urge to get out of the nest during the night.

18th day. A semblance of Figure hts appears in the nest as they kick, push, and grumble at each other. This action often involves several juveniles (Figure. 5).

Figure. 5. Juveniles of the edible dormouse on the 18th day of life

19th day. The ear canals of the young open. The auricles become dark in color. The coat becomes fluffy. There is a sharp increase in motor activity. According to Airapetyants (1983) and Lozan et al. (1990), the opening of the auditory canals occurs on the 15–17th days; according to von Koenig (1960), on the 12th day.
20–21st days. The upper teeth appear. The nostrils become sharply defined. According to von Koenig (1960), dormice begin to defecate outside the nest.

4.4 III stages (22–30 days)
It begins from opening the eyes and is associated with the development of behavioral and motor reactions outside the nest.
22nd day. Eyes open. The regeneration rings on the tail are hidden under the fur. Juveniles try to get out of the nest. According to Lozan et al. (1990), the eyes of the dormouse begin to open on the 17–18th day; according to the studies of Airapetyants and Fokin (1984), on the 18–21st day; according to von Koenig (1960), on the 21st day. From this time the juveniles begin to clean each other.
23rd day. Attempts to climb on branches (Figure. 6).

Figure. 6. Juvenile of the edible dormouse on the 23rd day of life

24th day. Young dormice climb the snags in the aviary, but their movements are extremely hesitant. Juveniles stagger strongly and often fall off the snags.
26–27th days. Thanks to the developed grasping reflex, the dormice confidently jump along the branches, however, balance problems are still noticeable. Juveniles often gnaw inedible solid objects, which is most likely caused by the growth of teeth. They begin to sniff solid food. Dormice show developed elements of the recognition ritual: meeting each other, they sniff each other's outer thighs.

The instinct of nest-building is manifested. According to von Koenig (1960), scent marking develops: urination and defecation are realized in one corner of the cage.
28th day. Juveniles begin to eat the usual food of adults with characteristic motor responses. According to Airapetyants (1983), dormice begin to eat solid food at 25 days of age.
30–32nd days. Identification, marking, grooming and other friendly encounters are formed. On the 30th day, young dormice show a new type of play behavior: they jump on each other and the mother from the back, trying to hold on, imitating the sexual behavior of adults. Such actions never caused aggressive reactions, so they were classified as friendly encounters. Von Koenig (1960) registered such behavior on the 33rd day, Airapetyants and Fokin (1984) on the 25–26th days.

4.5 IV stages (31–45 days)
Juveniles become independent of their mother. The transition to a solitary lifestyle. A full set of behavioral reactions characteristic of adults outside the breeding season is formed.
31st day. Young dormice begin to feed on solid food, while the female continues to feed them with milk and chewed food. According to Donaurov et al. (1938), in the Caucasus dormice switch to independent feeding already at 24–25 days of life. According to the observations of Airapetyants and Fokin (1984), the transition to solid food occurs earlier, on the 25th day.
34th day. Real Figure hts with bites and Figure hts in a ball (strict aggression) (Figure. 7).

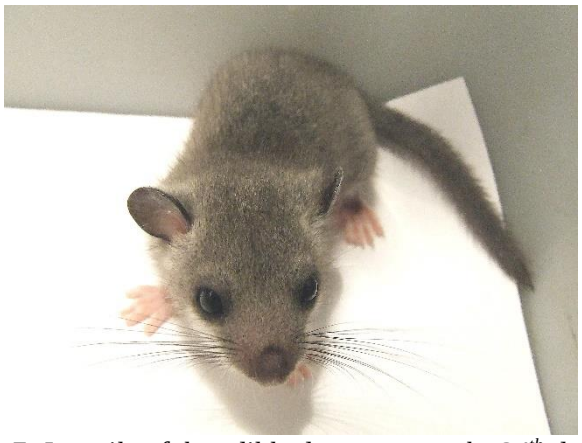

Figure. 7. Juvenile of the edible dormouse on the 34th day of life

35th day. Movements become fast and focused. The full species-specific recognition ritual, which is determined by the location of the glands on the dormouse's body, is formed: first, dormice sniff the sides at the base of the tail, then palm these places with their paws, and only after that proceed to the usual sniffing nose to nose (Vekhnik 2018).

36th day. The reaction of harboring of adult dormouse develops. The whole complex of behavioral elements characteristic of the feeding behavior of adult animals is observed.
38th day. Traces of juvenile moult appear. The coat becomes dull and uneven.

39–43rd days. End of lactation. In Austria, the lactation period ends at 47 days (von Koenig 1960); in the introduced population of England, weaning occurs at about four weeks of age (Morris 2004). Approximately the same lactation period is typical for the Caucasus (Donaurov et al. 1938, Airapetyants and Fokin 1984). Transition to nocturnal activity occurs. Feeding the food chewed by the mother is maintained until the litter is released into the mother's habitat (44–48 days). According to the observations of Airapetyants (1983), after the end of lactation, the litter still lives with the mother, going with her to feed. They leave the nest at the age of 40–45 days, find new shelters and aim to dispersal (Figure. 8).

Figure. 8. Juvenile of the edible dormouse on the 45th day of life

According to von Koenig (1960), postembryonic development ends on day **110.** However, the coat remains bluish and not brownish-grey like the old ones. Dormice can build nests like in adults.

5. Social relations in litters

The relations among the juveniles can be traced after leaving the nest. By the number of encounters of different types, it is possible to establish the division of siblings by rank into dominant and subordinate groups. The dynamics of social structure is shown by the example of one litter (Figure. 9). Sociograms of encounters within six juveniles (3 males and 3 females) from 33 to 47 days of development is given; in other studied litters, the development of relations proceeded similarly. The hierarchical structure of the litter was evaluated primarily on soft aggressive encounters, initiated by individuals (taking food away). The number of encounters of different types varied strongly during the observation period. The total number of encounters was maximal on the 36th day. The most numerous types were sexual encounters, being a part of benevolent encounters (Figure. 9d). Their number was more than double the number of usual benevolent encounters. Strict aggressive encounters were observed only in the first days of the formation of the hierarchical structure of the litter. An abrupt change of the elements of strict aggression by soft aggressive encounters testified to the early formation of mechanisms for the prevention of aggression and ritualized encounters. Scarce cases of strict aggression in litters, contribute to the survival of the maximum number of offspring.

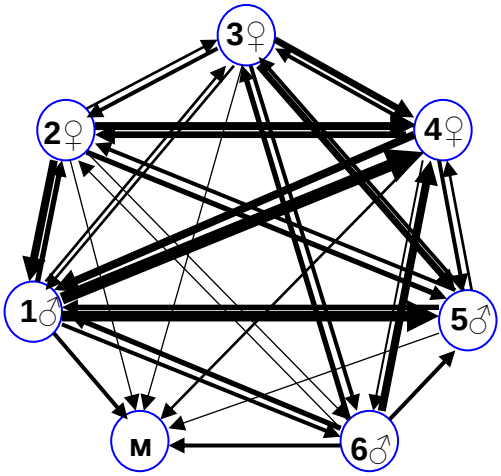

Figure. 9a. Soft aggressive encounters (n=127)

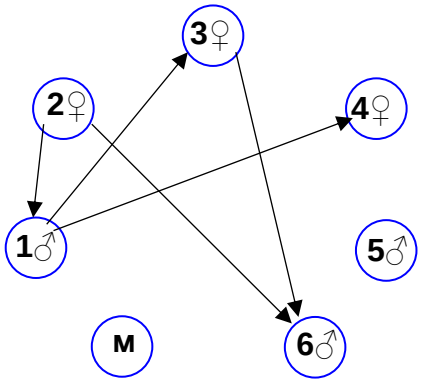

Figure. 9b. Strict aggressive encounters (n=5)

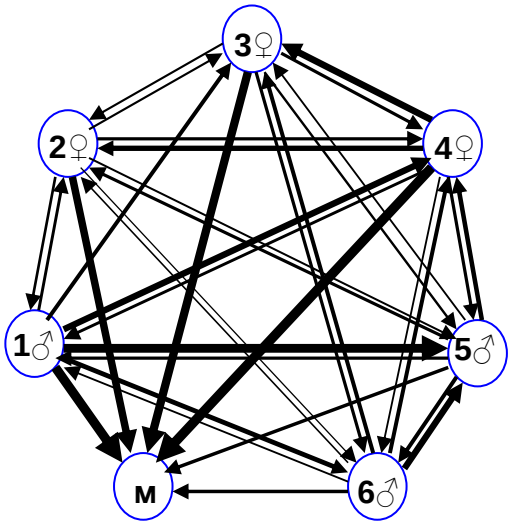

Figure. 9c. Benevolent encounters (n=56)

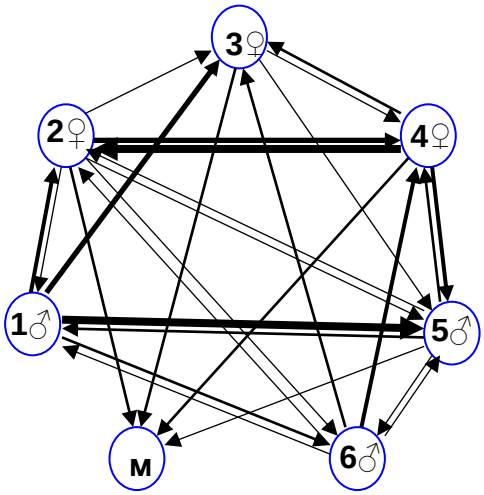

Figure. 9d. Sexual encounters (n=564)

Figure. 9. *Sociograms of interactions within a litter of the edible dormouse. Arrows mean number of encounters addressed to the particular siblings. Thinness is proportional to the number of contacts. Numbers mean a juvenile, M – mother.*

For convenience, the time for the development of intra-family relations was divided into three five-day periods. During every five days, a group of leaders may be determined. At the first stage (33–37 days), these were juveniles № 1 and № 3 (Figure. 10). Juveniles № 4 and № 5 were subordinates. Subdominant dormice № 2 and № 6 had weak social relations and were the initiators and recipients of a small number of encounters. The juvenile № 1 was the leader in terms of the number of benevolent and sexual encounters.

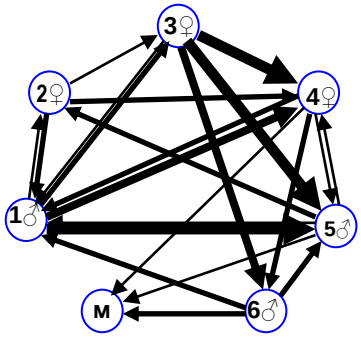

Figure. 10a. Soft aggressive encounters (n=44)

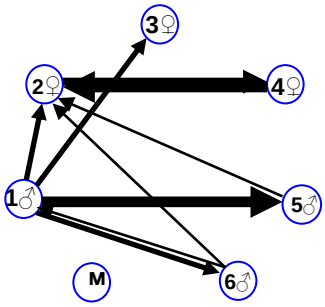

Figure. 10b. Benevolent encounters (n=20)

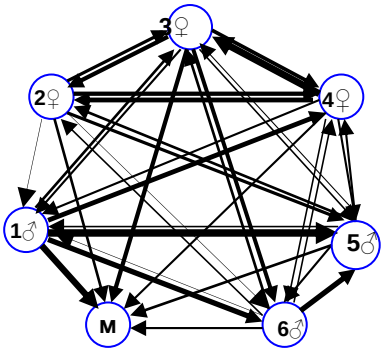

Figure. 10c. Sexual encounters (n=194)

Figure. 10*. Sociograms of interactions within the litter of the edible dormouse (33–37 days). Arrows mean number of encounters addressed to the particular siblings. Thinness is proportional to the number of contacts. Numbers mean a juvenile, M – mother.*

At the second stage of development (38–42 days), the dominant group also included the juveniles №1 and №3 (Figure. 11). The rest of the juveniles were subdominants. In terms of the number of friendly encounters, the dormouse №2 was in the leader, and the dormouse №1 and №4 were the first in sexual encounters.

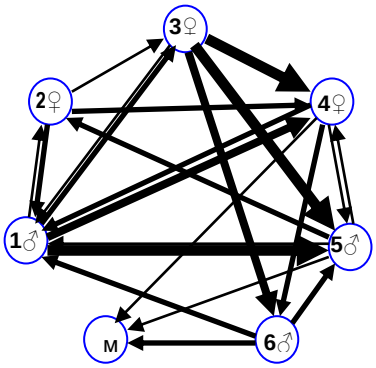

Figure. 11a. Soft aggressive encounters (n=43)

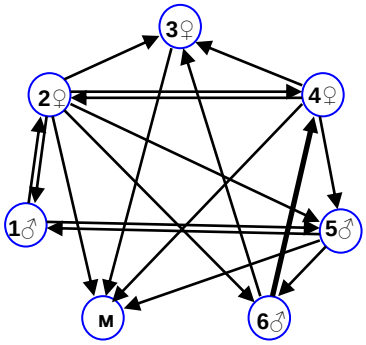

Figure. 11b. Benevolent encounters (n=19)

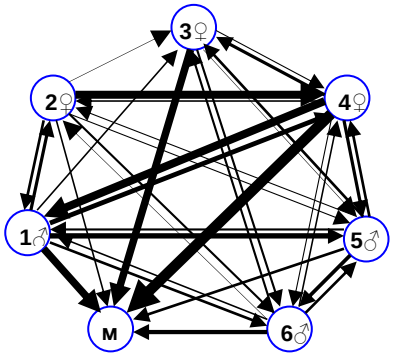

Figure. 11c. Sexual encounters (n=180)

Figure. 11. *Sociograms of interactions within the litter of the edible dormouse (38–42 days). Arrows mean number of encounters addressed to the particular siblings. Thinness is proportional to the number of contacts. Numbers mean a juvenile, M – mother.*

At the final third stage, the juvenile № 4 became dominant, juveniles № 1 and № 6 were in the subdominant group. Juveniles №2 and №3 were subordinates. There was a decrease in the total number of benevolent and sexual encounters (Figure. 12).

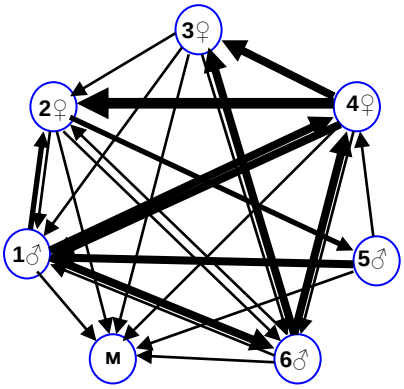

Figure. 12a. Soft aggressive encounters (n=39)

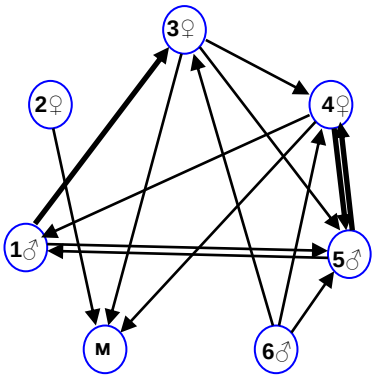

Figure. 12b. Benevolent encounters (n=17)

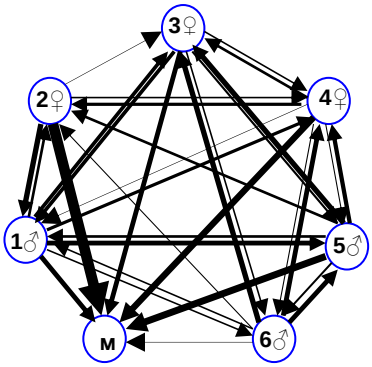

Figure. 12c. Sexual encounters (n=190)

Figure. 12*. Sociograms of interactions within the litter of the edible dormouse (43–47 days). Arrows mean number of encounters addressed to the particular siblings. Thinness is proportional to the number of contacts. Numbers mean a juvenile, M – mother.*

According to the observations, there is no clearly defined stepped hierarchy in litters. The dependence of the dominance of individuals on sex or body mass was not found. The very dynamic socio-hierarchical structure of litters contributes to the equable development of juveniles. Numerous encounters addressed to the female indicate the continuation of family relations even after the cessation of lactation. Thus, during social development behavioral traits reflect the ecological strategy of the species – ensuring the survival of all individuals in litters at a low reproductive potential.

In total, the formation of every behavioral act occurs gradually, supplemented during development with new elements. It is correlated with the chronological stages of physical development. The development of behavioral reactions flows synchronously in all juveniles in a litter. The exit from the nest, the process of feeding on solid food, and the beginning of the play behavior start in all the juveniles almost simultaneously. Many behavioral acts (nesting, feeding) begin as imitations of the mother.

Based on the observations, young dormice are most vulnerable at the third stage, when the level of physical development allows the animals to successfully orientate in the environment, but coordination of movements and experience is not enough to avoid external threats. Most juveniles may be killed by predators at this stage of development under natural conditions.

Periodicity of all stages of postnatal development is strictly limited. In different litters, the key stages of development pass with insignificant differences and serve as general species characteristics. Some differences in this timing may distinguish geographical populations. When compared with observations in the Caucasus region, where Airapetyants and Fokin (1984) and Donaurov et al. (1938) worked, as well as from Moldova (Lozan et al. 1990), the period of postnatal development of the dormouse in the Zhiguli population is more extended. The difference in the timing of the onset of individual stages of physical and mental development is up to seven days. However, the time of the onset of the key stages of postnatal development coincides with the data obtained by von Koenig (1960) for animals from the territory of Austria, except for the opening of the auricles, which occurs there already on the 12th day.

The period of early ontogenesis of the edible dormouse has species-specific features. These are feeding by chewed food and absence of visible concurrence inside litters. Dynamic and balanced rates of development, low level of aggression inside litters and high intensity of feeding contribute to the maximal survival rate of juveniles and preparing for the long hibernation.

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