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Review Article

A Review on the Edible dormouse reproduction (*Glis glis* Linnaeus, 1766)

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Abstract

The reproduction of the edible dormouse has a unique pattern. A characteristic feature of its reproductive ecology is the regular occurrence of reproductive failure years. This has been observed throughout the entire distribution range. Reproduction failure has different nature in eastern and western parts of the distributional range, depending on the tree stand composition. In the central and western parts of the area, the whole population and thus males and females do not invest in reproduction, if the yielding of broad-leaved tree species, mainly beech, is missing. During the years of beech mast failures, already most males remain reproductively inactive. The gonads remain in a prepuberty state, which is a typical pattern during hibernation in this species. In the eastern parts of the distribution area, reproductive success is determined mainly by females. The main factor is the appearance of oak sets, when the vast majority of female dormice are usually already pregnant. In years of reproductive failure, mating and pregnancy are observed. However, due to damage of the seed ripening the resorption of all embryos can be observed in dormice. In reproductive years, the litter size varies within wide limits (1-11). Several females can rear their offspring together, most likely the mothers are related. The periodicity of reproduction stages depends on the duration of the active period in different regions, sometimes showing a shift of up to two months. Costs of reproduction are revealed for males during and even before the mating period.

Keywords: Cost of reproduction, estrous cycle, *Glis glis*, male reproductive activity, mass embryonic resorption, reproductive failure

Introduction

Detailed studies of the edible dormouse (*Glis glis* Linnaeus, 1766) reproduction throughout the distribution range are currently limited to only a few points in the European part of the species area. However, differences in the characteristics of reproduction within the European genetic line of the species are pronounced. In this review, we compared data on the breeding biology and ecology of the dormouse from different studies, reaching from the west to the east of its distributional range.

A review of long-term observations in edible dormice shows a peculiar pattern of reproduction in this species. Years with successful reproduction are followed by years with a very low frequency of juveniles or even complete reproductive failure. Further, dormice seem to anticipate the future food availability (i.e., beech seeds and acorns). They invest in reproduction (both sexes) in the current year only if food and seeds later in the year will be abundant to allow fattening of the juveniles prior to their first hibernation. This phenomenon is widespread in this species and was observed in large parts of its distributional range (e.g., von Vietinghoff-Riesch, 1960; Bieber, 1998; Schlund et al., 2002; Pilastro et al., 2003; Ruf et al., 2006; Vekhnik, 2019). This pattern is strongly connected with the life history of this species. Indeed, dormice can live for up to 14 years (in England, Trout et al., 2015), allowing this species to compensate for years of skipped reproduction with an extraordinary life expectancy for an animal of this body size (Bieber & Ruf, 2009).

Seasonal timing of reproduction

A peculiarity of the reproductive cycle of the edible dormouse is the dependence of its duration on the period of hibernation. In fact, the duration period of sexually mature individuals in the population depends on climate conditions during reproductive years but may increase in southern areas and vary in individuals of different ages (e.g., Bieber et al., 2018). Within this short timeframe, animals mate, give birth to their young, wean them and accumulate fat reserves prior to their next hibernation (the scheme is given in Fig. 1).

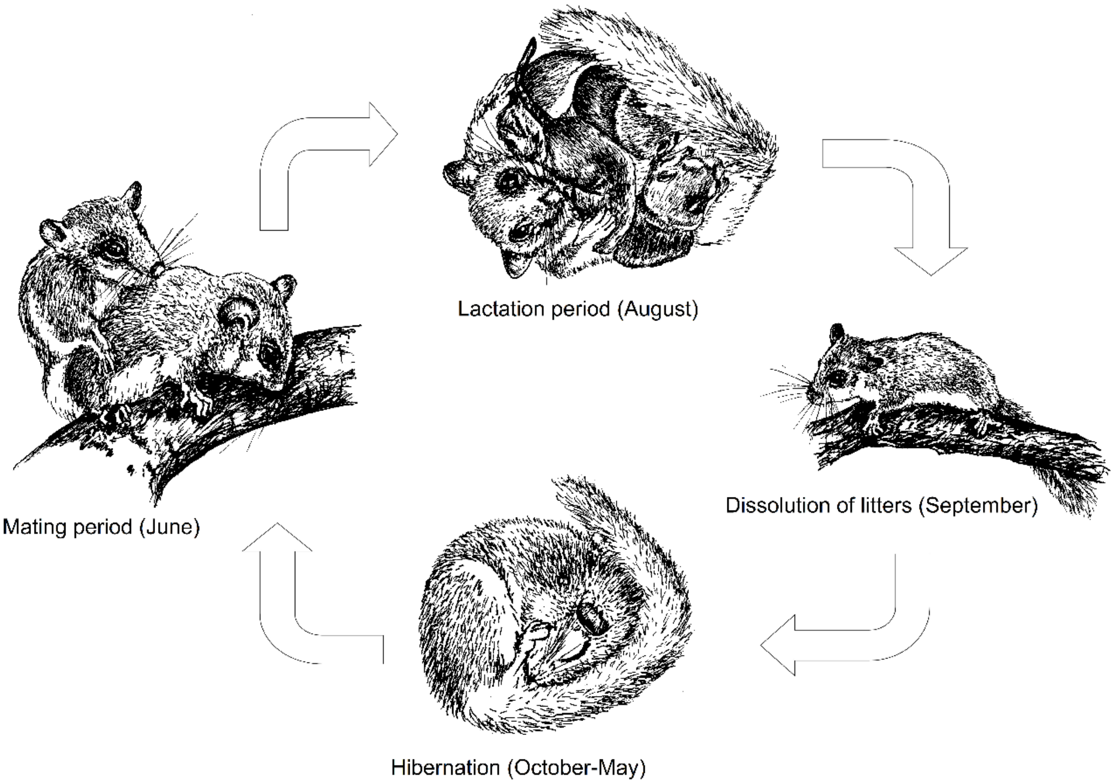

Figure 1. Reproductive period of the edible dormouse

Usually, males emerge from hibernation a week or two earlier than females (Airapetyants, 1983; Lozan et al., 1990; Bieber et al., 2018). In Moldova, the difference is 7-10 days (Lozan et al., 1990), in Germany and the Caucasus (Russia, Caucasian Reserve) it reaches four weeks (Donaurov et al., 1938; Schlund et al., 2002; Bieber & Ruf, 2009).

Dormice become sexually mature after the first wintering. Females usually emerge from hibernation ready to mate, at least in eastern populations. Only a small proportion of yearling females remain inactive for several days (Vekhnik, 2019).

Females retain the ability to give birth to juveniles once a year throughout their life (Geptner, 1932; Donaurov et al., 1938; von Vietinghoff-Riesch, 1960). The species has one estrous cycle per year (Airapetyants, 1983; Vekhnik, 2019). But there are indications of the probability of a second litter in one year. Sometimes very small juveniles are found at the end of the active season (Kryštufek & Flajšman, 2007; Vekhnik, unpublished data). Holcová Gazárková and Adamík (2016) registered two cases of second litters after the loss of the first ones. In captivity, repeated mating of females was observed in the case of the early loss of the first litters (≤ 3 weeks, von Koenig, 1960; Bieber, unpublished data). Based on body temperature data (implanted temperature-logger), two pregnancies in one female within one active season could be shown in a field study, too. Parallel nest box controls confirmed the probability of a second pregnancy if the first litter is lost within the first weeks (Bieber et al., 2017). This opportunity was indicated also by proestrus behaviour in females after parturition in the east of the range in Russia (Vekhnik, 2019).

Some of the adult males are ready for mating immediately, while the rest of them become active for a few days after hibernation (Lozan et al., 1990; Vekhnik, 2016). Yearling males usually need some time to develop the testis from the prepuberty state, and sometimes become active only after the second wintering (Spangenberg, 1935; Airapetyants, 1983; Lozan et al., 1990). According to the observations in the territory of the Zhiguli Mountains (Russia, the Middle Volga region), yearling males emerge much earlier than the older ones in May – early June, but they are not capable of mating immediately after awakening. Adult males may arise ready to mate in mid-June (Vekhnik, 2016).

The edible dormouse is a promiscuous species (Ściński & Borowski, 2008). The mating period almost throughout the whole range occurs mainly in July (Donaurov et al., 1938; von Vietinghoff-Riesch, 1960; Kadatskiy, 1964; Lozan et al., 1990; Hrabě, 1970; Schlund et al., 2002; Bieber & Ruf, 2009). The gestation period lasts approximately 30-40 days and lactation proceeds for 1.5 months (Rossolimo et al., 2001). Von Koenig (1960) observed in captive dormice the gestation period of ~31 days. The seasonal timing of breeding varies in the studied regions (Table 1):

Table 1. Approximate timing of the edible dormouse reproduction in different regions

Country	June	July	August	September	October	November	Source
Great Britain		mating	birth	weaning	weaning		Burgess et al., 2003
Italy (the Alps)		mating	birth	birth	weaning		Pilastro et al., 2003
Italy (Sicily)			mating	birth	birth	weaning	Milazzo et al., 2003
Germany	mating	birth	birth	weaning			Bieber, 1998
Austria	mating	mating	birth	weaning			Lebl et al., 2010
Luxembourg		mating	birth	birth	weaning		Schlichter et al., 2012
Czech Republic		mating	birth	weaning			Gaisler et al., 1977; Gazárková & Adamík, 2016
Slovenia	mating	birth	birth	weaning			Kryštufek et al., 2003
Poland		mating	birth	weaning			Ściński & Borowski, 2008
Lithuania	mating	birth	birth	weaning			Juškaitis & Augutė, 2015
Moldova, Ukraine (Dnieper Region)	mating	birth	weaning				Lozan et al., 1990
Turkey	mating	mating	birth	birth	weaning		Kryštufek & Vohralík, 2005
Georgia		mating	mating	birth	weaning		Geptner, 1932,

		🟩	🟩	🟥	🟦		Spangenberg, 1935
Armenia		mating	birth	weaning			Dal', 1954
Russia (the Caucasus)	mating	mating	birth	weaning			Donaurov et al., 1938, Tembotov, 1982
Russia (the Zhiguli Mts.)	mating	mating	birth	weaning			Vekhnik, 2020

Overall, there are no clear geographical patterns in the timing of the birth of juveniles through the distributional range. Probably, differences are partly caused by climatic conditions and differences in the duration of the active period. It is possible also that interannual differences have a definite effect on the results of studies. Fluctuations in the timing of the reproductive activity of dormice in each region may exceed the differences in timing between distant parts of distributional range. However, since the studies presented here embrace the data collected between the late 1930's up to today, the results may include a shift of the timing of emergence, due to climate change and global warming. For instance, in the territory of the Czech Republic, it has been shown that over twenty years a significant shift to an earlier onset of the active period occurred, which naturally may affect the timing of the breeding season (Adamík & Král, 2008). Similar results were obtained in the study in Germany (state of Hessia): The authors observed a time shift of emergence of four weeks from 1972 until 1999 (Koppmann-Rumpf et al., 2003) albeit there was also a change in the age structure of the population. More studies are needed to investigate the impact of climate change on the timing of reproduction in dormice.

Litter size

Litter size varies depending on the number of studied litters and forages conditions of a locality in certain years. Both the duration of the observation period and the differences in each studied point over the years can have a great influence. Table 2 provides information on the litter size from west to east.

Table 2. Litter size of the edible dormouse in different regions

Country	Litter size	References
England	6.8±2.16 (1–11) juveniles	Burgess et al., 2003; Morris & Morris, 2010
Germany	4.5 (1–9) juveniles 5–6 juveniles, up to 11	Von Vietinghoff-Riesch, 1960 Fietz et al., 2005
Austria	yearling females 4.3 ± 0.3 juveniles, two years and older 5.6 ± 0.4 juveniles	Lebl et al., 2010
Italy, Alps	5.3 ± 1.8; yearling females 4.7 juveniles, older females 5.8 juveniles	Pilastro et al., 1996, 2003
Italy, Sicily	5.5 ± 1.9 juveniles (2–8)	Milazzo et al., 2003
Czech Republic	5.5 (5-6) embryos, 4.9 (3-8) placental scars	Gaisler et al., 1977
Slovenia	5.8 embryos (4–9) and 4.9 juveniles (1–10)	Kryštufek et al., 2003, Kryštufek & Flajšman, 2007
Lithuania	5.9 ± 1.5(3–8) juveniles	Juškaitis & Augutė, 2015

Latvia	3–6 juveniles	Pilāts et al., 2009
Turkey	6.1 juveniles (1–12)	Kryštufek & Vohralík, 2005; Özkan et al., 2002
Moldova	1-10 juveniles	Lozan et al., 1990
Ukraine	3–8 juveniles	Sokur, 1960
Ukraine (Carpathians)	4 juveniles (3–7)	Turyanin, 1955
Ukraine (Dnieper region)	6.2 embryos and 6.5 placental scars (4–10)	Samarskiy & Samarskiy, 1980
Russia (Caucasus)	3–10 juveniles	Donaurov et al., 1938
Georgia (Transcaucasia)	3–8 juveniles	Geptner, 1932; Spangenberg, 1935
Iran	7.85±0.89	Naderi et al., 2013
Azerbaijan (Vartashen district)	2–7 juveniles	Meyer & Scholl, 1955
Armenia	3–8 juveniles	Dal', 1954; Sahakyan, 1964
Russia (Nizhegorodskaya Oblast)	3–5 (up to 10)	Puzanov, 1955
Russia (Tatarstan)	7 (N=1) juveniles	Popov, 1960
Russia (Samara Oblast)	1–8 juveniles	Unpublished data by Vekhnik

In almost all areas studied, the litter size changes within wide limits, which indicates the variability of the reproductive potential of females under the influence of different factors, regardless of the geographic location of a population's habitat. Variability was found also in the number of nipples, which amounts to 8-14 in different regions (Kryštufek, 2004; Naderi et al., 2014).

At a high population density, several females can rear their offspring together. Studies dedicated to this subject showed that communally breeding females are close kin: mother and daughters or sister pairs (Marin & Pilastro, 1994; Pilastro et al., 1996).

Reproductive skipping

A characteristic feature of the reproductive ecology in edible dormice is regular occurrence of reproductive failure years. This is observed throughout the entire distribution range (Airapetyants, 1983; Bieber, 1998; Schlund et al., 2002; Burgess et al., 2003; Fietz et al., 2005; Ruf et al., 2006; Lebl et al., 2010; Kryštufek, 2010; Vekhnik, 2019, etc.). In these failure years there are no offspring or the number of juveniles is minimal. Based on this, Pilastro et al. (2003) even concluded "to our knowledge, the fat dormouse is the first case, among small mammals, of breeding suppression occurring at the population level with such high frequency." Such a reproductive strategy leads to the fact that up to 96% of females participate in reproduction only once or twice in their life (Ruf et al., 2006). In the years without reproduction, dormice are able to hibernate from the beginning of summer, prolonging the total hibernation period to up to 11.4 months (Hoelzl et al., 2015). Long hibernation, low reproduction frequency and other factors contribute to extraordinary high life expectancy in comparison with other rodents of similar size (Bieber & Ruf, 2009; Turbill et al., 2013).

A clear adaptation among dormice of the investment into reproduction on the seed production of the broad-leaved tree species of Fagaceae family (i.e., European beech, *Fagus sylvatica*, oak, *Quercus spec.*) could be shown (e.g., Geptner, 1932; Ognev, 1947; Rossolimo et al., 2001; Bieber, 1997; Schlund et al., 2002; Fietz et al., 2005). In Sicily, an obligate dependence (r = 1) of the dormouse number on the yield of oak was found (Milazzo et al., 2003).

In **Italy**, in the south of the Alps, Pilastro et al. (2003) established a clear correlation between reproduction and the yield of beech. In mast-failure years, reproduction was completely absent. The reproductive activity was confined only to the years of high beech seed production. In masting years, the proportion of breeding females varied from 19.8 to 91.2%. But the authors cited also the study by Santini (1978), which stated that in Central Italy the rodent reproduces annually due to the abundance of food: pine cones, oak acorns, and ilex acorns.

In **central Germany (state of Hessia)**, in a study using wooden live traps, peaks of trapped dormice occurred in parallel with a high abundance of food in autumn, mainly beech seeds, in reproductive years. Large numbers of foraging juveniles, which leave their nests after weaning at this time, were responsible for this peak (Bieber, 1998). In a four-year study (1992, 1993, 1995, 1996) two years with successful reproduction (i.e. captured juveniles) paralleled by a beech mast could be observed (1992, 1995). In two years not a single juvenile could be captured. Interestingly, in one of these mast failure years, not a single male could be captured with tangible testis while in the second mast failure year 60% of the males were sexually competent. Thus, it seems likely that females can decide independently from males whether to invest into reproduction or not (Bieber & Ruf, 2004).

In **southwestern Germany (state of Baden-Württemberg)**, a correlation was found between the number of occupied nest boxes and the total yield, as well as for each of the three tree species *F. sylvatica, Q. petraea, Q. robur*. In turn, the proportion of occupied nest boxes correlated with the number of juveniles. More than 70% of males were active during the breeding years, and during the years of reproductive failure, their share did not exceed 22% (Schlund et al., 2002). In a pursued study considering more years, a strong correlation between beech mast and the occurrence of juveniles could be shown. Reproduction was low or even absent in four out of nine years (Ruf et al., 2006). It was confirmed that the proportion of active males depends on the yield of beech (Fietz et al., 2009) and the number of juveniles correlates with the number of active males (Fietz et al., 2004).

In A**ustria**, where the dependence of the intensity of reproduction on the yield of beech was also shown, in intermediate beech mast years proportion of reproducing females varied from 0.27 to 0.84. The dependence of fertility on the age of beech trees was revealed (until 60 year of tree age), maybe due to the fact that older trees produce more often more seeds (Lebl et al., 2011). A strong correlation between beech pollen (pollen /m^3 air) and a number of juveniles in nest boxes could be detected (Bieber & Ruf, 2004). This indicates that there is a reliable correlation between flowering and masting in European beech.

A connection of reproductive activity and beech yielding was found in **Slovenia** (Kryštufek et al., 2003; 2005). Males with enlarged testes were not caught here in lean years for beech. The number of sexually mature dormice individuals in the years of successful reproduction was always much higher than in the years without reproduction. It was revealed that, in contrast to most rodent species, the number of mature individuals in the years of successful breeding is always much higher than in the years of no breeding.

In the territory of the **Czech Republic**, the dependence of the number of dormice on the total yield of oak and beech, as well as the average temperature in May, was found (Adamík & Král, 2008). Barren females were revealed here, and participation in reproduction did not depend on age (Gaisler et al., 1977).

In **Moldova and Ukraine** (Middle Dnieper region), the proportion of breeding females averaged 61%, varying in different years from 21.2 % to 100 % (Lozan et al., 1987; Samarskiy & Samarskiy, 1980). In Moldova, only up to 10% of females remained barren.

In **Russia** (the Zhiguli Mts.), the proportion of breeding females ranged from 0 to 40% in years of poor seed harvest. A correlation was found between frosts during oak flowering and its fruiting, determined by overlapping dates (Vekhnik, 2019). The level of reproductive activity of males did not have a decisive importance and amounted on average to 94.1% of sexually active males every year. Similar studies by Snigirevskaya (1953) in the middle of the last century in the same territory also showed years of absence of juveniles.

It is interesting to note that in the introduced population of **Great Britain**, the same patterns are observed as in the continental part of the range. Reproduction is associated with beech harvests. There is a correlation between litter size with beech yield. In turn, the yield of beech is determined by the climatic conditions of the previous year: a dry June / July is required for flower bud formation (Burgess, 2002; Burgess et al., 2003; Morris, 2003). Moreover, the alternation of reproductive and non-reproductive years is even more strict than within the native species range. Often in non-reproductive years, juveniles do not occur at all (Morris & Morris, 2010).

It may be an oversimplification to assume that in the reproductive cycle of the dormouse, the years of reproduction are always followed by the years of its complete absence. Despite years with no juveniles mentioned by traditional hunters (Valvasor, 1994), studies by Kryštufek et al. (2005) in Slovenia, based on the absence of gaps in the distribution of age classes of skulls during morphological analysis, showed that the complete cessation of reproduction does not occur there. On the other hand, in many beech forest areas (northern Italy, GB, Germany, and Austria) however, the complete skipping of reproduction and inactivity of males in mast failure years could be observed (Burgess, 2002; Pilastro et al., 2003; Bieber & Ruf, 2004; Ruf et al., 2006; Hoelzl et al., 2016). Most likely the abundance of beech, oak, or alternative feeding plants may be responsible for the observed differences in reproductive investment. Interestingly, it could be shown that within a large deciduous forest dormice avoid nest boxes in pure beech stands. A mixed composition of trees (e.g., coniferous trees) might provide a more constant food supply in mast failure years of beech (Cornils et al., 2017).

This is illustrated by a long-term study in **Lithuania.** In 25 years (1990-2014) juveniles were not recorded in nestboxes only in 2004, 2005, 2008 and 2010 (Juškaitis & Augutė, 2015). During four years of targeted research, reproductive failure was not observed. Breeding was noted mostly at adult females (90%) and only at 20% of yearling females.

Regulation of male reproductive activity

Male reproductive activity correlates with the yielding of broad-leaved tree species, mainly beech, in central and western parts of the distributional range (Bieber, 1997; Burgess et al., 2003; Kryštufek et al., 2003; Fietz et al., 2004). During the years of beech mast failures, most males remain reproductively inactive. The volume of testes in active males in lean years is much smaller (Schlund et al., 2002). Thus, the decision to invest into the development of gonads in early summer precedes the absence of high-calorie seeds during the reproductive season (Bieber, 1998; Schlund et al., 2002; Burgess et al., 2003; Pilastro et al., 2003; Fietz et al., 2004; Ruf et al., 2006).

The timing of hibernation may have an additional influence on male reproductive activity (Burgess, 2002; Schlund et al., 2002). After especially plentiful harvests, the dormouse may accumulate fat reserves until the end of October, and then the next year the duration of hibernation increases. Late arousal from hibernation inhibits the development of testes, as a result of which males are unable to mate.

In the eastern periphery of the range in Russia, no significant influence of the level of reproductive activity of males on the intensity of reproduction was revealed (Vekhnik, 2019). Active males were numerous every year. Sexual activity was related to age. Yearling males participating in reproduction for the first time had the smallest individual duration of the mating period (up to 34 days); two-year-old males participated for the longest time (up to 48 days). The period of individual reproductive activity of three-year-old males reached 39 days. A characteristic feature of the reproduction of one-year-old males was found: they participate in reproduction depending on the body mass. Since such a relationship was not reliably noted in other age groups, it can be argued that the main role here is played not by energy reserves, but by the age of the animals and the date of birth determines the body mass of one-year-old males for the next year and the time of recruitment into reproduction (Vekhnik, 2016).

Regulation of female reproductive activity

The structure of the estrous cycle was studied in the easternmost population in the Zhiguli Mts. (Russia). All phases of the estrous cycle, with the exception of proestrus, which can be easily missed at the beginning of the reproductive season, are very long. The pattern of the estrous cycle differs between reproductive and non-reproductive years (Fig. 2) (Vekhnik, 2019).

Almost all females emerge from hibernation in the estrous phase, which lasts at least 18–23 days in different years. In a few individuals, anestrus is recorded for at least 18 days or proestrus for at least three days. The duration of pregnancy is 30–32 days. In reproductively successful years after the birth of juveniles, diestrus is observed for at least 12 days. Then females have proestrus before hibernation for at least 15 days. In years of reproductive failure, mating and pregnancy are observed in the eastern population. After a gestation period of variable duration, resorption of all embryos occurs, accompanied by the transition of females to the meta-estrous phase for at least 25 days and appropriate changes in body mass. Then, before hibernation, females enter the diestrus for at least 25 days. After resorption, there is no proestrus period before hibernation. Thus, in the years of suppression of reproduction in the reproductive cycle the birth of posterity does not occur or the proportion of juveniles is sharply reduced despite the gestation of most females.

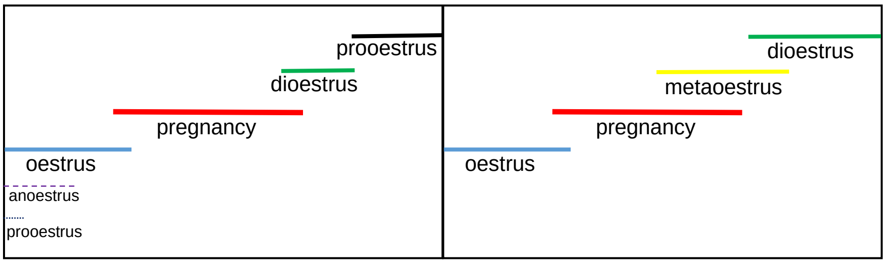

Figure 2. Scheme of the estrous cycle of the edible dormouse during an active period in reproductive years (left) and the years of reproductive failure (right).

When analyzing the data obtained from Russia (Vekhnik, 2019, 2020), significant distortions are obviously caused by census methods using live traps or nest boxes. Over the three years of parallel studies using both methods, the ratio of reproducing (lactating) and non-reproducing females was the opposite: while in live traps the proportion of females with resorption significantly exceeded the proportion of lactating females, in nest boxes the proportion of lactating females was higher (unpublished data by Vekhnik).

Currently, the study carried out by Vekhnik in an oak forest (2019) on edible dormice is the first to describe the phenomenon of mass resorption of embryos in mammals. Resorption of embryos in most species of placental mammals is usually observed in few individuals under unfavorable conditions and most often only some of the embryos are affected (Lobkov, 1999; Tumanov, 2003; Krackow, 1992; Owusu et al., 2010 and many others). In the edible dormouse on the periphery of the range, complete resorption of embryos is regular and becomes the main element of the regulating of the birth rate and the basis for the formation of population cycles.

However, some studies indicate a more widespread occurrence of the phenomenon of mass resorption in this species. Mass embryonic resorption may have a decisive influence on the reproduction of dormice in eastern Poland (Ściński & Borowski, 2005; Jurczyszyn, personal communication). Von Vietinghoff-Riesch (1960), who conducted a study on dormice in Germany, assumed that the resorption of embryos may contribute to reproductive failure.

Partial resorption of embryos in dormice was studied in the Caucasus (Russia) (Donaurov et al., 1938). The proportion of reduced embryos in one female at dissection was up to 19.3%. Barren females were also noted (4.7%). The authors consider embryonic mortality and barrenness in some females to be the main mechanism of population regulation inherent to this species. Most one-year-old females do not participate in reproduction.

In southwest Germany (Baden-Württemberg), with a similar level of male reproductive activity, the proportion of females varied significantly (Fietz et al., 2004).

Interestingly, in captivity, some animals may not breed despite good physical conditions (von Koenig, 1960). In a study by Yiğit (2001), females did not give birth to juveniles in the laboratory despite males' reproductive activity and the constant availability of a wide variety of food.

The reproductive success of females can also be influenced by multiple paternity (Moska et al., 2021). On a study site in Austria, the number of sires per offspring group ranged from two to four (Weber et al., 2018). For other species, it has been proven that females are able to increase reproductive success by increasing the number of matings, as was shown by the example of rodents and bats (Fox et al., 2008; Bergeron et al., 2011).

Cost of reproduction

From the standpoint of the life cycle theory, the cost of reproduction is one of the main factors of participation in breeding and total reproductive output (Williams, 1966; Roff, 2002; Stearns, 1992). As the edible dormouse is a hibernator, evidence of the cost of reproduction should be very clearly manifested due to severe time restrictions.

A significant cost of reproduction is obvious during the analysis of the body mass of dormice. According to a study by Fietz et al. (2004), the body mass of males participating and not participating in reproduction did not differ after arousal from hibernation. In Central European populations of dormice, a significant decrease up to 31% of body mass is observed in males during the mating season (Bieber, 1998; Schlund et al., 2002; Fietz et al., 2004; Sailer & Fietz, 2009). Moreover, significant loss of body mass begins even before the mating period (Bieber, 1997; Sailer & Fietz, 2009). In dormice, body mass directly translates to body fat reserves (Schaefer et al., 1976).

Fietz et al. (2004) considers that in addition to energy costs arising from mating, the protection of territory, and fighting during the rutting period, males have physiological costs of reproduction, such as depression of the immune system associated with a high level of plasma testosterone, the development, and maintenance of secondary sex characteristics, sperm, and ejaculate production. In active males, the body condition deteriorates during the rut, while in inactive males it remains unchanged.

In Italy, the body mass of males in non-reproductive years, in general, is higher than in the reproductive years (Pilastro et al., 2003). In Germany, the body mass of females and males at the beginning of a reproductive failure year is higher than at the same time point in a reproductive year (Bieber, 1998). But in reproductively successful years body mass before hibernation becomes higher than in non-reproductive years because of better food conditions (Fietz et al., 2005).

Fietz et al. (2004, 2005) studied the energetic constraints of the reproductive activity of males. Body condition (body mass/tibia length) directly after emergence from hibernation did not differ between sexually active and quiescent individuals. Then reproducing males exhibited a significant decrease in body condition. Sexually active males had a median oral temperature of 34.2°, in sexually quiescent it was 28.8°C (Fietz et al., 2004). A temperature of about 30 ° C, is considered a critical minimal body temperature for testes to develop, which requires a high-energy diet to maintain (Jallageas & Assenmacher, 1983). Beechnuts may represent a high-quality food resource rich in lipids and proteins, which enables sexually active males to partially compensate for the costs of reproduction, including thermoregulatory expenses (Fietz et al., 2005).

Thermoregulatory costs are connected with lowered ability to enter daily torpor (Jallageas & Assenmacher, 1983; Ruf & Bieber, 2020a). During the breeding years, males usually do not enter the torpor state in summer due to their reproductive activity (Fietz et al., 2004). To reduce energy losses, during the rutting period dormice even have a special strategy – huddling behavior, which promotes less energy-consuming thermoregulation during the mating period (social thermoregulation) (Fietz, 2012; Fietz et al., 2010; Koppmann-Rumpf et al., 2012; Ruf & Bieber, 2020b).

The costs of reproduction of females manifested as losses of body mass during lactation were shown in Italy, accounting for approximately 5-10% of the female body mass (Pilastro et al., 1996). When comparing the costs of reproduction of one-year-old and older females, calculated as the difference in body mass between the birth and weaning of juveniles, no differences in this value were found, although the difference in the weight parameters of females of both age groups was 15–20 g. Differences in the mortality rate of young and mature animals were also insignificant. In Germany, females were significantly heavier in the non-reproductive year (1993), than in the reproductive year (1992) (Bieber, 1998).

In one-year-old females, age can limit reproductive success. The reproductive success of females after the first winter is significantly lower than that of females after the second wintering and older ones, which is expressed in the proportion of females reproducing (Lebl et al., 2011), the size of the litters, and in the later date of births (Pilastro et al., 1996). The difference in body mass after parturition between yearling and older females is approximately 30 g (Pilastro et al., 1996; Lebl et al., 2011; Ruf et al., 2006).

Body mass at first hibernation in Italy determined the body mass and fecundity of females in subsequent years. Some of the yearlings with a body mass of less than 100 g did not reproduce at all (Pilastro et al., 1996). The body mass of yearling reproducing females was always more than 110 g. In non-breeding one-year-old females, body mass was in some cases less than 85 g. It is interesting that Ognev wrote about the same issue in 1947: "Individuals that survived the winter, due to the weakness of the body, and did not receive sufficient fat reserves in the fall, lag behind the normal reproduction period; females give a reduced number of juveniles, some of which die" (Ognev, 1947; translated from Russian). In other studies, in females, including pregnant individuals, significant changes in body mass were not found.

Role of the chemical composition of forages in the regulation of breeding intensity

In the optimum range, mainly in beech-dominated forests, reproductive success is determined during the beginning of the flowering of the beech and depends on the abundance of flowers and buds. Many authors consider the abundance of flowers and tree buds of beech in spring and early summer, which is determined in this species six months before fruiting, to be a trigger factor that stimulates the growth of dormouse testes (Bieber, 1998; Burgess, 2002; Pilastro et al., 2003; Fietz et al., 2005; Ruf et al., 2006).

In oak-dominated forests mostly in the east of the species area, reproductive success is determined by the appearance of oak ovaries, when the vast majority of female dormice are usually already pregnant. Oak flowering cannot be a predictor of the beginning of reproduction, because unlike in the case of beech, it is not possible to predict the yield of acorns from the intensity of flowering (Bogdziewicz et al., 2017). In both cases, the lactation period in general ends usually when tree seeds begin to fall, in the period of the maximum abundance of ripe tree seeds – in late August-early September. Such adaptation ensures maximum availability of matured feeds for weaned offspring.

In the published data, the role of ripening seeds is discussed from two sides. A number of researchers (Bieber, 1998; Schlund et al., 2002; Pilastro et al., 2003) consider immature forages to be a trigger factor, stimulating physiological reserves for the reproduction of dormice, the existence of which for mammals living in "pulsating" communities was argued by Boutin et al. (2006). On another side, immature seeds are the main source of high-energy food (Ruf & Bieber, 2020a). Studies of the reproduction in different types of biotopes have shown that the natality rate depends on the proportion of beech and oak in the tree stand composition, since even in unripe seeds, the fat content is incomparably higher than in other forages, for example, in fruits (Bieber & Ruf, 2009). In this case, tree seeds serve as both energy sources and predictors of future food availability.

This conclusion is confirmed by the experimental work of Sailer and Fietz (2009). Studies of dormouse digestion and metabolic rate have shown that the level of nutrient assimilation did not change during the entire period of activity. Thus, it is the content of high-energy substances in the diet that serves as a necessary factor in compensating for high energy costs during the breeding season before prolonged hibernation.

Fietz et al. (2009) also conducted studies on lipid composition in basic forages. They found a high content of linoleic acid in beech nuts. Linoleic and oleic fatty acids are the main component of subcutaneous fat during hibernation, and the content of linoleic acid determines body mass loss of dormice during hibernation (Bieber et al., 2014; Fietz et al., 2005). Therefore, for hibernation, the decisive factor is not quantity, but the quality of food.

The results of experiments on artificial feeding did not give the same results. The study by Lebl et al. (2010) in Austria, conducted in a beech-dominated forest, showed that in males on supplementary feeding plots, the rate of reproductive activity was significantly higher as well as the number of females with litter significantly increased. The researchers suppose that dormice use the energy content of food (e.g., seed buds) as an environmental signal for investment into reproduction.

At the same time, the study of Borowski et al. (2018) in a forest with a predominance of Scots pine (*Pinus sylvestris*) in Poland gave another result. Supplementary feeding did not affect reproduction, body condition or population dynamics of dormice. Also, differences in the number of offspring or sex ratio were not found.

In the peripheral population of the dormouse of the Zhiguli Mts. (Russia), unripe tree seeds play the role of a source of high-quality food. Besides years of acorn harvesting, successful reproduction was observed there also entirely due to the rare abundant harvests of hazel (Vekhnik & Vekhnik, 2018). Under laboratory conditions, females gave offspring without eating of acorns (unpublished data by Vekhnik). Also, the energetic role of acorns was confirmed when analyzing the age structure and life cycles of females. At medium yields of oak and low yields of hazel in the same biotopes, in some three-year-old females resorption occurred, while others gave birth to juveniles. In the case that the number of immature acorns would have only a trigger function, the birth of juveniles or resorption would always be synchronized in most of the females (Vekhnik &Vekhnik, 2018). Similarly, a decisive role of hornbeam (*Carpinus betulus*) fructification in dormice reproduction was observed in Poland (Ściński & Borowski, 2008).

Studies of the lipid composition of acorns and nuts were conducted in the peripheral population of the Zhiguli Mts. (Vekhnik et al., 2019). The total lipid content in acorns was significant both at the beginning and at the end of maturation. In nuts, at the beginning of growth, the lipid content was lower, but during ripening, it increased many times. During the maturation of acorns, the proportion of triacylglycerols significantly increased. The composition of fatty acids was different in acorns and nuts. In the initial period of fruit, ripening differed mainly in two acids, oleic and linoleic. The first acid in July prevailed in hazel seeds, and the second in oak seeds. After ripening linoleic acid remained predominant in acorns. In hazelnuts, the fatty acid composition was significantly reduced, and oleic acid became the main fatty acid.

Sharp changes in the composition and content of lipids during the maturation of basic forages may have a significant impact on the periodization of breeding in dormice. Sufficient content of energy-rich neutral lipids in immature acorns, almost the same as in mature seeds, may contribute to the successful course of pregnancy. A high proportion of triacylglycerols in mature seeds ensures the successful wintering of juveniles and the survival of females after lactation. Triacylglycerols are the main constituents of animal fat (Nelson & Cox, 2000). Linoleic acid has a positive effect on hibernation (Ruf & Arnold, 2008).

So, the role of immature tree seeds in the reproduction of the edible dormouse is both the supply of necessary nutrients and in the synchronization of deciduous tree species fruiting and the growth of young, for which ripe seeds serve as the main food source and provide maximum survival in case of possible competition with adults. Even immature acorns contain a sufficient amount of lipids to support the vital activity of rodents. Thus, the females rear the young on the basis of feeding on immature seeds, and the independent young dormice have an abundant supply of mature seeds.

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