Regulation of reproduction rate in terrestrial placental mammals

Victoria A. Vekhnik
Samara Federal Research Scientific Centre RAS, Institute of Ecology of Volga River Basin RAS, Togliatti, Russia

E-mail: ivavika@rambler.ru

Abstract. Mechanisms of regulation of reproduction are studied in a limited number of mammalian species, but these studies are extremely important for the conservation of rare animals. This study is a review of the data on reproductive biology of over 120 mammalian species. Four hierarchical levels of regulation of reproduction rate in mammalian females are identified: regulation of the number of embryos, regulation of the oestrous cycle, regulation of the number of females participating in reproduction, and regulation of reproduction rate at the population level. This classification makes it possible to draw a number of conclusions: (1) the mechanisms of reproductive regulation may be similar in distant taxonomic groups; (2) completely different regulatory mechanisms can be realized simultaneously in the same species at various levels; (3) the higher the level of regulation, the greater the number of individuals participating; (4) the nutritional factor is of integral importance and affects reproduction rate at all levels; (5) at the population level, the mechanism of anticipatory reproduction evolves, being a natural regulatory mechanism. The studies of reproductive restrictions in males may appear as a fruitful area for obtaining new data about regulation of reproduction rate in populations. The role of male reproductive activity in the regulation of reproduction seems highly underestimated.

1. Introduction
Nowadays, the regulation of population density in mammals is among the central and most studied issues of the animal ecology. Several hypotheses of population regulation, widely used by ecologists, explain the mechanism of autoregulation of the number of mammals (see the review [1]). At the same time, a narrower problem, regulation of reproduction attracts the researchers’ attention much less often; the studies are mainly empirical and are usually performed for commercial or endangered species. However, in order to identify general regularities in the regulation of reproduction, it is necessary to structure the existing knowledge. Reproduction is undeniably key to the survival of all species on earth, whether they live in situ or ex situ [2]. In this study, a scheme for regulating the intensity of mammalian reproduction depending on external factors is proposed based on the analysis of literature data on more than 120 mammalian species, as well as our own data on rodents (figure). Of course, any classification is artificial to some extent, but the identification of the levels of regulation of reproduction clearly reveals the "blank spots" and the most promising areas of research.
2. Levels of regulation of the reproduction rate in mammals

Four levels of regulation of reproduction in females of terrestrial placental mammals may be distinguished, identified mainly during observations in the wild, including by non-invasive methods. This review presents some examples of such regulation at each level, some of them are taken from the monographs by W V Holt et al. [3] and P Comizzoli et al. [4], as well as reviews by B W Brown [5], J L Vaughan and A Tibary [6], and S Amstislavskiy and Yu Ternovskaya [7]. In a number of cases, information on the same species is given at different levels based on the studies performed by different authors.

2.1. Regulation of the number of embryos

The most common and well-known mechanism for regulating the number of mammalian offspring is embryonic resorption. It is observed in most of the studied mammalian species: least weasel (Mustela nivalis), marbled polecat (Vormela peregusna), Eurasian otter (Lutra lutra) [8]; wild boar (Sus scrofa) [9], European hare (Lepus europaeus) [10], spotted souslik (Spermophilus suslicus), little ground squirrel (S. pygmaeus), russet ground squirrel (S. major), yellow ground squirrel (S. fulvus), red-cheeked ground squirrel (S. erythrogenys), long-tailed ground squirrel (S. undulatus) [11]; deer mouse (Peromyscus maniculatus) [12], yellow-necked mouse (Apodemus flavicollis) [13], bank vole (Clethrionomys glareolus) and northern red-backed vole (C. rutilus) [14, 15], house mouse (Mus musculus) [16], greater cane rat (Thryonomys swinderianus) [17], and many other species. In rabbit (Oryctolagus cuniculus) in the wild, 50% of embryos and more can be absorbed or not implanted [18]. In the speckled ground squirrel, the limitation of the annual growth rate can occur due to the resorption of all embryos in certain females [11]. The maximum manifestation of the effect of resorption on the population of the species is mass resorption of embryos in the edible dormouse (Glis glis), in which all embryos in all captured females can be resolved in lean years [19].

In camelids, embryonic mortality is often associated with the inability of the right uterine horn to maintain pregnancy. Studies have shown that in most cases there is migration from the right to the left horn or death of embryos [20]. In addition, South American camelids have mechanisms that prevent multiple pregnancies: the birth rate of twins is less than 1% in these species [6].

![Scheme of hierarchical levels of regulation of reproduction rate in mammals.](image)

Figure. Scheme of hierarchical levels of regulation of reproduction rate in mammals.

Studies of several rodent species support the adaptive effect of diet on the sex ratio of offspring [16, 21]. Under the conditions of food limitation, the number of litters with the predominance of females decreases [22, 23, 24]. But Krackow [16] observed that in laboratory hamsters, the susceptibility of males to embryonic mortality in litters increased with dietary restrictions.

Embryonic developmental disorders may be associated with other nutritional conditions. Poisons in plants can strongly influence on embryo development [25]. In sheep and mice, an increase of dietary protein reduces the total number of embryos or disrupts their development [26].
The manifestation of various maternal effects, or epigenetic influences of parental phenotypes on offspring, may be attributed to the same level of regulation, as shown in the review by A V Badyaev [27].

Various pauses in the course of reproduction, limiting the number of descendants in a certain period of time, is another way of the regulation of the number of offspring. Various types of reproductive delays have been confirmed for more than one hundred mammalian species [28]. Reproductive delays occur between mating and fertilization, fertilization and implantation of the embryo, as well as during the development of the embryo. Delayed implantation of embryos is known in bears and mustelids [29]. Long-tailed weasel (Mustela frenata), African striped weasel (Poecilogale albinucha), American badger (Taxidea taxus), least weasel, and marbled polecat are able to reproduce as early as 3-5 months and give offspring only the next year due to delayed implantation, and stoat (Mustela erminea) females are ready for fertilization at the age of 20 days [7]. In bats, all three types of delays described above are present [30, 31].

2.2. Regulation of the oestrous cycle
The structure of the mammalian oestrous cycle determines the periods when females are able to participate in reproduction. It is determined not only by the physiological characteristics of animals, but may be significantly modified depending on environmental factors.

The triggering effect of the presence of a male on stimulation of oestrus is widespread in mammals. It has been proven for such species as bush dog (Speothos venaticus) [32], common yellow-toothed cavy (Galea musteloides) [33], and the European water vole (Arvicola terrestris) [34]. Presenting an unfamiliar male can cause abortion and transition to oestrus (the "Bruce effect") in newly mated females of the laboratory mice [35]. Conversely, presentation of an unfamiliar male, as well as his smell, can serve as a stimulus to suppress oestrus [36].

Social interactions may influence the age of onset of reproductive activity in female mammals. Acceleration of oestrus occurs in laboratory-reared brown rats (Rattus norvegicus) after presenting a male [37]. The role of male "preparing" pheromones in the onset of the oestrous cycle after parturition in livestock ("ram effect") is known for domestic pigs (Sus scrofa) [38], sheep (Ovis aries) [39, 40] and goats (Capra hircus) [41].

In a number of social species, the structure of the oestrous cycle of females and the ability to produce offspring may be influenced by the hierarchical position of individuals. For example, in African wild dog (Lycaon pictus) and Ethiopian wolf (Canis simensis), the dominant female is able to suppress the reproduction of subordinate individuals [42]. In the colonies of Damaraland mole-rat (Cryptomys damarensis) and the naked mole-rats (Heterocephalus glaber), usually one female and one male are active [43, 44].

Conversely, keeping females in groups, as well as the smell of other females, can inhibit the onset of oestrus in mammals [12], for example, in house mouse [45] and white-footed mouse (Peromyscus leucopus) [46].

Nutrition can significantly influence the structure of the oestrous cycle. Cows with a higher body condition score had shorter intervals of postpartum anoestrus in comparison to cows with a lower body condition score regardless of whether bulls were present or not [47]. In the white-footed mouse, a decrease in nutrient intake reduces the probability of oestrus [48].

2.3. Regulation of the number of females participating in reproduction
The participation of females in reproduction depends both on external conditions and on the physical condition of a particular individual. The effect of the body mass of females on participation in reproduction is widely known. In the red squirrel (Sciurus vulgaris), the reproductive success of both males and females depends on the weight parameters before the mating period [49]. In camel females, for the onset of sexual maturity, it is necessary to achieve body mass equal to 60% from the body mass of adults, depending on the quality of nutrition [50].

The life history theory, first formulated by D Williams [51] and generalized by D Roff [52] and S K Stearns [53], is the most widespread theory generalizing the regulation of reproduction at this level. This theory explains variations in the size of living organisms at birth, growth rate, age of maturation,
number of descendants and parental input, survival rate and life span. The energy cost of breeding is considered one of the decisive factors in reproduction. For example, in the Asian elephant (*Elephas maximus*), the relationship between reproduction and survival of adults was confirmed, positive at the beginning of life, but negative after reaching the age of 30 years [54]. In the American red squirrel (*Tamiasciurus hudsonicus*), the ability to reproduce increases up to four years and remains constant thereafter, while the possibility of giving birth to a second litter in fruitful years increases with age [55].

In hibernating species, the periodicity of reproduction is of great importance for the reproduction rate. Individuals that breed earlier have greater reproductive success, which has been shown by the example of common hamster (*Cricetus cricetus*) and ground squirrels [56, 57]. At the same time, in early awakening females, the duration of the reproductive period does not increase [58].

### 2.4. Regulation at the population level

Seasonality in reproduction is one of the brightest and most common mechanisms of adaptation of species to environmental conditions and the availability of resources at the level of local populations [59]. The stimuli for the beginning of reproduction may be the length of daylight hours and the amount of precipitation. In the Northern Hemisphere, day length determines the start of the breeding season in most mustelids [7] and bears [60].

For canines, whose range extends over large areas and continents, the breeding period varies in different regions (see review by Jewgenow and Songsasen [61]). For example, in the North America, the wolf (*Canis lupus*) become reproductively active as day length begins to increase [62], but in the South America the maned wolf (*Chrysocyon brachyurus*) reproduces when the day length decreases [63]. In rabbits, during short favorable periods of heavy rainfall, several broods are born in a row [64].

Another widespread phenomenon is the dependence of reproduction on the yield of available forage. For example, the abundance of food is much more important for reproductive success than the weight and age of the red squirrel females. In fruitful years, red squirrels that have grown offspring can produce second broods [55]. Laine and Henttonen [65] showed a positive correlation between the number of flowers and the density of the rodent population next year in ten plant species.

At this level of regulation, we can see the regulation according to the principle known as anticipatory reproduction. This is the birth of the optimal number of offspring before the actual harvest of the main food, causing synchronization of the beginning of independent feeding of the young with the period of maximum food abundance. In red squirrel and common squirrel (*Sciurus vulgaris*), reproduction precedes the abundant forage harvest, predicting it [66]. The white-footed mouse (*Peromyscus leucopus*) is able to "anticipate" the appearance of periodic cicadas and accelerate reproduction to the peak of their numbers [67]. In the eastern chipmunk *Tamias striatus*, in forests dominated by the American beech *Fagus grandifolia*, population growth is synchronized with the peak of seed abundance [68].

In a number of studies, similar patterns are not classified as anticipatory reproduction. In the white-footed mouse, the largest proportion of juveniles preceded the years of the peak abundance [69], as observed also for European hare inhabiting Australia. The period of abundance of vegetation is observed in September-December, and the period of the maximum number of pregnant females falls on July [10]. A typical example of anticipatory reproduction is the edible dormouse, whose breeding precedes beech harvests [70]. A similar way of regulation of reproduction was revealed in such a widespread species as the yellow-necked mouse [71].

### 3. Regulation of male reproductive activity

The regulation of the reproductive activity of male mammals has been studied incomparably less than that of females. Only for seventeen species from analyzed for the review the data were presented for both males and females. For example, in hibernating hamsters, males are known to awake earlier than females [58]. The reproductive biology of male elephants is known due to the unique phenomenon of must and unusual reproductive anatomy. They have reproductive problems described in females, such as social suppression of gonadal function [54]. In alpacas, the androgen-dependent mechanism of readiness for mating depends on the diet [20]. The constant presence of females has an inhibitory
effect on the reproductive activity of male llamas [50, 54]. Since the level of fertility in females is consistently high, the level of reproductive activity in males plays a decisive role [6]. Males of the African wild dog are able to produce sperm throughout the year, but of poor quality outside the breeding season [62]. The reproductive activity of male American red squirrels is highly dependent on both current and future food abundance [72]. In other obligate hibernators, such as Spermophilus saturatus, and small ground squirrels (Citellus pygmaeus), as well as marmots (Marmota sp.), the reproductive activity of males is affected by the success of fattening in the previous fall [11, 73]. The previous study showed that in the yellow-necked mouse the reproductive activity of males has the decisive importance, like it is observed in the edible dormouse in the optimum of the range [70]. There is a number of studies of male reproductive biology from the standpoint of the theory of life cycles. These studies evidence that the energy costs of reproduction for males are similar or even higher than that for females; however, little is known about this phenomenon (see reviews [72] and [74]).

4. Conclusion

Structuring the system of different mechanisms of regulation of reproduction made it possible to draw a number of generalizations. The mechanisms of regulation of reproduction rate may be similar in systematically distant taxonomic groups. In the same species, completely different regulatory mechanisms at different levels may be realized simultaneously. The higher the level of regulation, the greater the number of individuals it covers. For example, the costs of reproduction may be negligible in fruitful years [58].

The nutritional factor is of integral importance; it affects the reproduction intensity at all levels. It may act both indirectly and directly, i.e. by influencing the number of offspring in a certain female.

At the population level, a mechanism of anticipatory reproduction appears, but not as a unique phenomenon, but as a natural regulatory mechanism that serves as adaptation to changing feeding conditions. In studies from this point of view, the number of species with such regulation may be revealed significant.

A significant amount of new data and the disclosure of new patterns may be obtained by studies of reproductive restrictions in males. The role of male reproductive activity in the regulation of reproduction is extremely underestimated. The huge number of ovulating-induced mammalian species supports the role of males in the regulation of the reproduction rate [5, 7, 34, 75, 76, 77, etc.]. At this stage, it can be assumed that participation in reproduction in males is much more dependent on external conditions than that of females.

Acknowledgements

The author is grateful to Vladimir P. Vekhnik for the invaluable help at all stages of this study and to Prof. Sergey V. Saxonov and Dr. Olga A. Rozentsvet for the discussion of the manuscript.

References

[1]. Rogovin K A, Moshkin M P 2007 Autoregulation of abundance in mammalian populations (touches to a long-term picture) Zhurnal obschey biologii 68 244–267
[2]. Holt W V, Brown J L and Comizzoli P 2014 Reproductive Science as an Essential Component of Conservation Biology Reproductive Sciences in Animal Conservation, Advances in Experimental Medicine and Biology ed WV Holt et al. (New York: Springer Science+Business Media) chapter 8 pp 3–14
[3]. Holt W V, Brown J L, P. Comizzoli (ed.) 2014 Reproductive Sciences in Animal Conservation (Springer Science+Business Media New York)
[4]. Comizzoli P, Brown J L, Holt W V (ed) 2019 Reproductive Sciences in Animal Conservation (2nd ed.) (Springer Nature Switzerland AG)
[5]. Brown B W 2000 A review on reproduction in South American camelids Anim. Reprod. Science 58 169–195
[6]. Vaughan J L, Tibary A 2006 Reproduction in female South American camelids: A review and clinical observations Small Ruminant Research 61 259–281
[7]. Amstislavsky S, Ternovskaya Y 2000 Reproduction in mustelids Anim Reprod Sci. 60-61 571–581
[8]. Tumanov I L 2003 Biological features of carnivorous mammals in Russia (Saint-Petersburg: Nauka)
[9]. Ivantenko I D 1956 Postnatal development of a wild boar in relation to environmental conditions (Stalingrad)
[10]. Stott P and Harris S. 2006 Demographics of the European hare (Lepus europaeus) in the Mediterranean climate zone of Australia Mamm. Biol. 71 214–226
[11]. Lobkov V A 1999 Spotted ground squirrel of the northwestern Black Sea region (Odessa: Astroprint) 1247–1256
[12]. Bruce H M 1966 Smell as an Exteroceptive Factor J. Anim. Sci. 25 83–87
[13]. Nurullina A N 1957 Seasonal cycle of reproduction of the yellow-necked mouse and the bank vole in oak forests of Balashovskaya Oblast Proceedings of the Forest Institute 35 122–136
[14]. Vorontsov N N 1961 Ecological and some morphological features of bank voles (Clethrionomys Tiletius) of the European northeast Proceedings of the Zoological Institute of the Academy of Sciences of the USSR 29 101–130
[15]. Ivanter E V 1975 Population ecology of small mammals of taiga north-earth of USSR (Leningrad: Nauka)
[16]. Krackow S 1992 Sex ratio manipulation in wild house mice: The effect of fetal resorption in relation to the mode of reproduction Biology of Reproduction 47 541–548
[17]. Owusu B A, Adua E K, Awotwi E K, Awumbila B 2010 Embryonic resorption, litter size and sex ratio in the grasscutter, Thyromyns swinderianus Animal Reproduction Science 118 366–371
[18]. Brambell F W R 1942 Intra-uterine mortality of the wild rabbit, Oryctolagus cuniculus (L.) Proc R Soc Lond, B Biol Sci 130 462–479
[19]. Vekhnin V A 2019 Effect of food availability on the reproduction in edible dormice (Glis glis L., 1766) on the eastern periphery of the range Mammal Research 64 423–434
[20]. Fernández-Baca S 1993 Manipulation of reproductive functions in male and female New World camels Anim. Reprod. Sci. 33 307–323
[21]. Rosenfeld C S and Roberts R M 2004 Maternal diet and other factors affecting offspring sex ratio Biology of Reproduction 71 1063–1070
[22]. Rivers J, Crawford M 1974 Maternal nutrition and the sex ratio at birth Nature 252 297–298
[23]. Labov J B, Huck U W, Vaswani P, Lisk R D 1986 Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters (Mesocricetus auratus) Behavioral Ecology and Sociobiology 18 241–249
[24]. Kwong W Y, Wild A E, Roberts P, Willis A C, Fleming T P 2000 Maternal undernutrition during the preimplantation period of rat development causes blastocyst abnormalities and programming of postnatal hypertension Development 127 4195–4202
[25]. McEvoy T G, Robinson J J, Ashworth C J, Rooke J A and Sinclair K D 2001 Sinclair feed and forage toxicants affecting embryo survival and fetal development Theriogenology 55 113–129
[26]. Parr R A, Davis I F, Fairclough R J, Miles M A 1987 Overfeeding during early pregnancy reduced peripheral progesterone concentrations and pregnancy rate in sheep J. Reprod. Fertil. 80 317–320
[27]. Badyaev A V Maternal Effects as Generators of Evolutionary Change: A Reassessment Anim. Reprod. Sci. 33 307–323
[28]. Orr T J, Zuk M 2014 Reproductive delays in mammals: an unexplored avenue for post-copulatory sexual selection Biol. Rev 000–000.
[29]. Renfree M B, Shaw G 2000 Diapause Annu. Rev. Physiol. 62 353–375
[30]. Oxberry B A 1979 Female reproductive patterns in hibernating bats Journal of Reproduction and Fertility 56 359–367
[31]. Borisenko A V 2000 Comparative morphology and evolution of the female reproductive system and breeding biology of smooth-nosed bats (Vespertilionidae, Chiroptera). PhD thesis. (Moscow)

[32]. Porton I J, Kleiman D G, Rodden M D 1987 A seasonality of bush dog reproduction and the influence of social factors on the estrous cycle. J. Mammal. 68 867–871

[33]. Touma C, Palme R, Sachser N 2001 Different types of oestrous cycle in two closely related South American rodents (Cavia aperea and Galea musteloides) with different social and mating systems Reproduction 121 791–801

[34]. Nazarova G G, Potapov M A, Evsikov V I 2007 The probability of estrus and mating in the water vole (Arvicola terrestris) depends on the physical condition of the females, sexual experience and the behavior of the mating partners Zoologicheskiy zhurnal 86 1507–1512

[35]. Parkes A S and Bruce H M 1961 Olfactory stimuli in mammalian reproduction Science 134 1049

[36]. Parkes A S and Bruce H M 1962 Pregnancy block in female mice placed in boxes soiled by males J. Reprod. Fertil. 4 303.

[37]. Hughes R L 1964 Effect of changing cages, introduction of the male, and other procedures on the oestrous cycle of the rat. Wildlife Res. 9 115

[38]. Brooks P H, Cole D J, 1970 The effect of the presence of a boar on the attainment of puberty in gilts J. Reprod. Fertil. 23 435–440

[39]. Schinckel P G 1954 The effect of the ram on the incidence and occurrence of oestrus in ewes Australian Vet. J. 30 189

[40]. Izard M K, Vandenbergh J G 1982 The effects of bull urine on puberty and calving date in crossbred beef heifers J. Animal Sci. 55 1160–1168

[41]. Shelton M 1960 Influence of the presence of a male goat on the initiation of oestrous cycling and ovulation of Angora does J. Animal Sci. 19 368

[42]. Van den Berghe F, Paris D B B P, Van Soom A, Vandenbergh J M H, Kirkpatrick R L 1981 Relative Sensitivity of Reproductive Activity and Body-fat Level to Food Restriction in White-footed Mice The American Midland Naturalist 106 305–312

[49]. Lee T H 2001 Mating behavior of the Eurasian red squirrel (Sciurus vulgaris Linnaeus, 1758) in Hokkaido, Japan Mammalia 65 131–142

[50]. Sumar J B 1996 Reproduction in llamas and alpacas Anim Reprod Sci 42 405–415

[51]. Williams G C 1966 Natural selection, the costs of reproduction and a refinement of Lack’s principle Am. Nat.100 687–690

[52]. Roff D A 1992 The evolution of life histories (New York: Chapman and Hall)

[53]. Stearns S C 1992 The Evolution of Life Histories (Oxford: Oxford University Press)
[54]. Brown J L 2014 Comparative Reproductive Biology of Elephants Reproductive Sciences in Animal Conservation. Advances in Experimental Medicine and Biology ed WV Holt et al. (New York: Springer Science+Business Media) chapter 8 pp 135–169

[55]. Descamps S, Boutin S, Berteaux D, Gaillard J M 2007 Female red squirrels fit Williams’ hypothesis of increasing reproductve effort with increasing age J. Anim. Ecol. 76 1192–1201

[56]. Millesi E, Hubert S, Everts L G and Dittami J P 1999 Reproductive decisions in female European Ground squirrels: factors affecting reproductive output and maternal investment Ethology 105 163–175

[57]. Vasilyeva N A, Chabovsky A V 2017 Making of reproductive decisions in the context of a “fast” life cycle (by the example of yellow souslic Spermophilus fulvus Journal of common biology 78 3–14

[58]. Franceschini-Zink C, Millesi E 2008 Reproductive performance in female common hamsters Zoology 111 76–83

[59]. Carey C 2014 Climate Change, Extinction Risks, and Reproduction of Terrestrial Vertebrates Reproductive Sciences in Animal Conservation, Advances in Experimental Medicine and Biology ed WV Holt et al. (New York: Springer Science+Business Media) chapter 3 pp 35–54

[60]. Spady T J, Lindburg D G, Durrant B S 2007 Evolution of reproductive seasonality in bears Mammal Rev 37 21–53

[61]. Jewgenow K and Songsasen N 2014 Reproduction and Advances in Reproductive Studies in Carnivores Reproductive Sciences in Animal Conservation, Advances in Experimental Medicine and Biology ed WV Holt et al. (New York: Springer Science+Business Media) chapter 10 pp 205-240

[62]. Asa C, Valdespino C 1998 Canid reproductive biology: an integration of proximate mechanisms and ultimate causes Amer. Zool. 38 251–259

[63]. Rodden M, Rodrigues F, Bestelmeyer S. 2004 Maned Wolf (Chrysocyon brachyurus) Foxes, wolves, jackals and dogs. Status survey and conservation action plan ed Sillero-Zubiri C, Hoffman M, Macdonald DW (Cambridge: IUCN/SSC Canid Specialist Group) pp 38–43

[64]. Martínez-Gómez M, Juárez M, Distel H, Hudson R 2004 Overlapping litters and reproductive performance in the domestic rabbit Physiol. Behav. 82 629–636

[65]. Lane K, Henttonen H 1983 The role of plant production in microtine cycles in northern Fennoscandia Oikos 40 407–418

[66]. Boutin S, Wauters L A, McAdam A G, Humphries M M, Tosi G and Dhandt A A Anticipatory reproduction and population growth in seed predators 2006 Science 14 1928–1230

[67]. Marcello G J, Wilder S M, Meikle D B 2008 Population dynamics of a generalist rodent in relation to variability in pulsed food resources in a fragmented landscape Journal of Animal Ecology 77 41–46

[68]. Bergeron P, Réale D, Humphries MM, Garant D 2011 Evidence of multiple paternity and mate selection for inbreeding avoidance in wild eastern chipmunks J. Evol. Biol. 24 1684–1695

[69]. Falls J B, Falls E A, Fryxell J M 2007 Fluctuations of deer mice in Ontario in relation to seed crops Ecol. Monographs 77 19–32

[70]. Ruf T, Fietz J, Schlund W, Bieber C 2006 High survival in poor years: life history tactics adapted to mast seeding in the edible dormouse Ecology 87 372–381

[71]. Vekhnik V A, Vekhnik V P, Rozentsev O A, Bogdanova E S 2019 Possible relations between reproduction of the yellow-necked mouse (Sylvaemus flavicollis) and oak yield Russian Journal of Theriology 18 33–42

[72]. Lane J E, Boutin S, Speakman J R and Humphries M M 2010 Energetic costs of male reproduction in a scramble competition mating system Journal of Animal Ecology 79 27–34

[73]. Arnold W and Dittami J 1997 Reproductive suppression in male alpine marmots Anim. Behav. 53 53–66

[74]. Partridge L, David Gems D and Withers D J. Sex and Death: What Is the Connection? Cell 120 461–472
[75]. Weir B J 1974 Reproductive characteristics of hystricomorph rodents Symp. Zool. Soc. Lond. 34 265–301
[76]. Jackson C R and Bennett NC 2005 Is the Natal mole-rat (Cryptomys hottentotus natalensis) a spontaneous or induced ovulator? J. Mammal. 86 1–6
[77]. Pelican K M, Wildt D E, Pukazhenthi B and Howardet J G 2006 Ovarian control for assisted reproduction in the domestic cat and wild felids Theriogenology 66 37–48