

Breeding by young-of-the-year females in common dormouse, *Muscardinus avellanarius*, populations in Lithuania

Rimvydas Juškaitis

Institute of Ecology, Vilnius University, Akademijos 2, LT-2600 Vilnius, Lithuania (e-mail: juskaitis@ekoi.lt)

Received 18 Mar. 2003, revised version received 25 Aug. 2003, accepted 25 Aug. 2003

Juškaitis, R. 2003: Breeding by young-of-the-year females in common dormouse, *Muscardinus avellanarius*, populations in Lithuania. — *Ann. Zool. Fennici* 40: 529–535.

Breeding by young-of-the-year females comprised 12.7% of 479 breeding cases of the common dormouse (*Muscardinus avellanarius*), recorded in two Lithuanian populations during 1981–2002. These females were born in late May–early July, and their age was 60–80 days at their first parturition. Average litter size of young-of-the-year females was smaller than of adult females (3.6 and 4.1 juveniles, respectively). A significant negative correlation between dormouse population density in spring and the percentage of breeding cases involving young-of-the-year females was established ($r = -0.76$; $p < 0.001$). When population density is low, young-of-the-year females have a greater possibility of finding free territories in which to breed. Overwinter survival of breeding and non-breeding young-of-the-year females from the same cohort did not differ in either of the populations. Early born females can breed in the year of their birth and do not reduce their chances of surviving the winter, but adult established females suppress their breeding at moderate population density.

Introduction

Age at first reproduction varies widely among small mammals, depending on species life history, season, population density or phase of cycles (e.g. Negus *et al.* 1977, McAdam & Millar 1999, Prevot-Julliard *et al.* 1999, Yoccoz & Ims 1999, Ergon *et al.* 2001, Lambin & Yoccoz 2001, Millar 2001). Females become reproductively active either in the year of their birth (usually spring-born animals) or in the following year (usually autumn-born animals). Microtine rodents are well known for their precocious reproduction (Tkadlec & Zejda 1995). Females

born early in spring may not only produce five to six litters in the year of their birth, but their own young can also reproduce without delay (Lambin & Yoccoz 2001). High turnover rate and short life span are characteristic features of Microtine voles as well as of many other species of small mammals (e.g. Christian 1971, French *et al.* 1975, Tkadlec & Zejda 1995).

Dormice (Gliridae) are unusual among small mammals of similar body size because of their longevity and low population turnover rate. In the wild, solitary individuals of the common dormouse (*Muscardinus avellanarius*) can reach an age of up to 5–6 years (Juškaitis 1999a), the

fat dormice (*Glis glis*) up to eight years (Schlund *et al.* 2002). In most cases, dormice produce only one litter per season (Storch 1978), and even total reproduction failures have been observed in fat dormouse populations in certain years (Bieber 1998, Schlund *et al.* 2002). Second litters are possible only in the southern parts of the distribution ranges of some dormouse species (Storch 1978, Bertolino *et al.* 2001). However, common dormouse females may produce two litters in almost all distribution ranges during a given breeding season (*see* Storch 1978, Juškaitis 1997a).

According to Storch (1978), all European dormice become sexually mature after their first or second hibernation. However, breeding by young-of-the-year females as an exceptional case is known among common dormice (Likhachev 1966, Catzefflis 1984, Juškaitis 1997a; S. Büchner unpubl. data). Likhachev (1966) linked it with very favourable feeding conditions and Juškaitis (1997a) to decreased population density. The aim of the present paper was to analyse breeding by young-of-the-year females in two Lithuanian common dormouse populations, and explore its relation to population density. The survival of females and their offspring during the following winter was also investigated.

Material and methods

Studies of two isolated common dormouse populations were carried out at study site A (south-western Lithuania, Šakiai district; 55°03'N, 23°04'E) in 1984–1990 and in 1997–2002, and at study site B (eastern Lithuania, Molėtai district; 55°09'N, 25°21'E) in 1984–1993. For characteristics of birth time, data from study site A in 1981–1983, before nestboxes were laid out in a grid system, were also used.

Site A, with an area of 60 ha and 262 nestboxes (274 nestboxes in 1999–2002), covered about 22% of the whole habitat occupied by the common dormouse population in that locality. The forest here was middle-aged (30–80 years old), with a great diversity of mixed tree stands. Within the study site, mixed birch (*Betula pendula*) stands with Norway spruce (*Picea abies*) and black alder (*Alnus glutinosa*), ash (*Fraxinus*

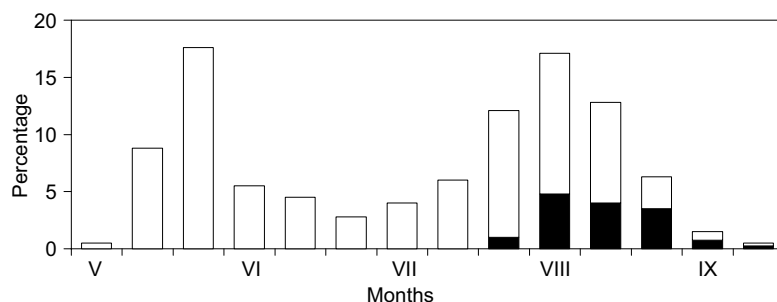
excelsior) stands with aspen (*Populus tremula*), and pure Norway spruce stands were prevalent. There was also a mixed Norway spruce stand with oak (*Quercus robur*) at the southern edge of the site. The understorey consisted mainly of hazels (*Corylus avellana*) and in some places, buckthorn (*Frangula alnus*).

Site B, with an area of 85 ha and 341 nestboxes, covered approximately 17% of the whole habitat occupied by the common dormouse population in that locality. Mature oak stands (100–130 years old) with Norway spruce, and in some places with maple (*Acer platanoides*) and aspen, were prevalent in most parts of this site. In the eastern part of the site, aspen stands (40–60 years old) grew with Norway spruce. There were also small plots of Norway spruce, aspen and grey alder (*Alnus incana*) in this area. Hazel prevailed in the understorey.

At both study sites, standard wooden nestboxes for small hole-nesting birds were placed in a grid system every 50 meters (*see* schemes in Juškaitis 1997b, 2002). The density was four boxes per 1 ha. The boxes were checked once a month from April until October, and twice a month in May and September (in some years also in October). All dormice caught were marked with aluminium rings (the straightened plate was 2.5 × 8.0 mm). The rings were placed on the right hind leg over the ankle. Suckling young weighing less than 10 g were marked by amputation of one toe phalanx, and ringed if caught later. All the animals were weighed and their sex and age determined.

The age of juveniles in litters was estimated according to the development of external features and body weight (Likhachev 1971, Slastionenko 1990). Juveniles born in May–July were regarded as early born juveniles. Dormice were considered adults if they had survived at least one hibernation. Unmarked young-of-the-year females were distinguished from adult dormice according to lower body weight (Juškaitis 2001) and additional indicators: greyer fur coloration, narrower tail and earlier moulting time (R. Juškaitis unpubl. data). Breeding females were considered to be not only the ones found in nestboxes with litters, but also those that were caught pregnant or with visible nipples, having given birth to their litters in natural nests.

Fig. 1. Birth time of litters in the common dormouse in Lithuania ($n = 398$). Litters by young-of-the-year females are designated by filled bars, adult overwintered females by empty bars.



The spring population density was determined by dividing the total number of overwintered individuals, caught during the whole active season, by the trapping area of the study site (Flowerdew 1976). The trapping area was considered as 64 ha at site A and 90 ha at site B. This was calculated by adding a 50-m wide boundary strip to the sides of the study sites which were not delimited by forest edge (or forest road at site A). Dormice caught at least once during the following active season were considered to have overwintered successfully, and consequently survival rate of dormice during the winter was estimated as the proportion of successfully overwintered animals that had been caught in autumn (August–October). Early born juveniles were already sedentary in August–October (Juškaitis 1997b), and their survival could be compared with survival of adult dormice. Some juveniles, born in August, could leave the study areas and their survival might have been slightly underestimated.

A total of 479 cases of breeding common dormice were registered at study sites A and B in 1981–2002. Among them, 61 cases of breeding by young-of-the-year females were found. Dates of birth were established in 398 breeding cases, including 54 examples of young-of-the-year female breeding.

Results

In the two Lithuanian common dormouse populations investigated, breeding by young-of-the-year females comprised 12.7% of all breeding cases registered in 1981–2002. Most often such females gave birth in mid-August–early September (Fig. 1). Individual marking has shown

that the majority of these females were born in June (late May–early July), and their age was 60–80 days when they gave birth to their first litters. Litter sizes of young-of-the-year females ($n = 53$) varied from 1 to 5 juveniles, averaging 3.63 ± 1.04 (mean \pm SD) juveniles, while average size of a litter born to an adult female in August–September was larger (4.09 ± 1.06 ; range 1–7; $n = 142$; two-way ANOVA: for female age, $F_{1,191} = 6.52$; $p = 0.011$; for study site, $F_{1,191} = 0.98$; $p = 0.323$; interaction, $F_{1,191} = 0.00$; $p = 0.985$). However, the two populations investigated did not differ in litter size significantly, although it was a little larger at site A.

Breeding by young-of-the-year females was more frequent at site B than at site A (19.2% ($n = 213$) and 7.5% ($n = 266$) of all registered breeding cases, respectively; $\chi^2_1 = 14.64$; $p < 0.001$). At site B, where average population density was lower, 25.3% of early born females ($n = 166$) bred, while at site A ($n = 169$) the comparable figure was 8.9% ($\chi^2_1 = 16.00$; $p < 0.001$). The assumption was made that breeding by young-of-the-year females could be related to lower population density. A significant negative correlation between dormouse population density in spring and the percentage of breeding cases involving young-of-the-year females was established in pooled data from both populations ($r = -0.57$; $n = 17$; $p = 0.017$). This relationship was strongly influenced by data from site B in 1987, when no case of breeding by young-of-the-year females was registered, despite the fact that the spring population density was only 0.5 adults ha^{-1} (Fig. 2). When this outlier was omitted, a closer relationship ($r = -0.76$; $n = 16$; $p < 0.001$) was obtained between the population density in spring and breeding by young-of-the-year females. A very similar correlation ($r = -0.74$;

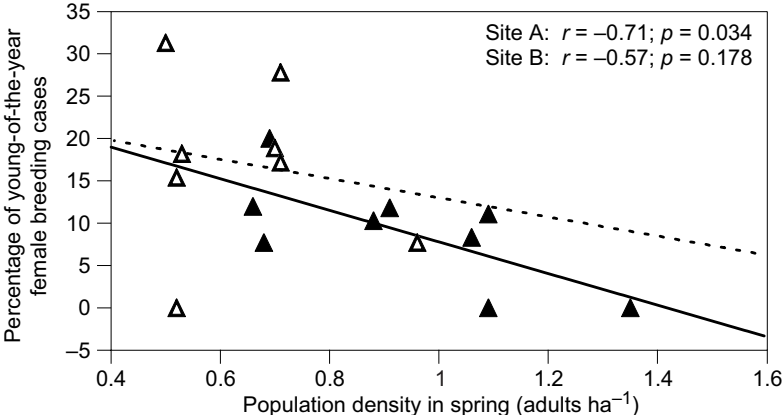


Fig. 2. Correlation between common dormouse population density in spring and the proportion of young-of-the-year females breeding at study site A (filled triangles and continuous line) and site B (empty triangles and dashed line). This relationship is strongly influenced by the data from site B in 1987 (see comments in the text).

$n = 16$; $p = 0.001$) was found between density of overwintered females and breeding by young-of-the-year females.

Overwinter survival of breeding and non-breeding young-of-the-year females from the same cohort did not differ in either of the populations ($\chi^2_1 = 0.01$; $p = 0.925$ and $\chi^2_1 = 0.00$; $p = 0.969$ for sites A and B, respectively; Table 1). At both study sites, survival of breeding young-of-the-year females was a little higher than in adult females, which gave birth in August–September (Table 1), although differences were not statistically significant in either of the populations ($\chi^2_1 = 0.57$; $p = 0.451$ and $\chi^2_1 = 1.41$; $p = 0.235$ for sites A and B, respectively). At study site A, dormouse survival was higher than at site B in all female groups compared, but differences were not significant ($\chi^2_1 = 0.33$ – 1.72 ; $p = 0.566$ – 0.190). Survival was comparatively low among offspring of both young-of-the-year females and

adult females, which gave birth in August–September (Table 1). However no regularity could be found: the lowest survival was among offspring of young-of-the-year females at site A and offspring of adult females at site B.

Discussion

Common dormice usually start to breed after their first hibernation when they are about one year old. Solitary cases of breeding by young-of-the-year females have been observed in different parts of the common dormouse distribution range: Switzerland (Catzeffli 1984), Germany (S. Büchner unpubl. data), the Tula and Moscow regions of Russia (Likhachev 1966). In Lithuania, there were many more such cases registered among the large amount of data collected during my long-term studies. It is possible that some

Table 1. Overwinter survival of females from different demographic groups and their offspring in two common dormouse populations in Lithuania.

Demographic group	Survival of females and their offspring, % (<i>n</i>)		
	Breeding young-of-the-year females	Adult females, which gave birth in August–September	Non-breeding early born young-of-the-year females
Site A			
Females	42.9 (14)	32.6 (89)	41.6 (154)
Their offspring	4.3 (46)	14.3 (203)	–
Site B			
Females	34.2 (38)	23.6 (72)	33.9 (124)
Their offspring	14.3 (91)	6.5 (138)	–

researchers did not register breeding by young-of-the-year females because of the difficulty of distinguishing unmarked breeding young-of-the-year females from adult overwintered females. S. Büchner (unpubl. data) has also stressed this problem.

Because of hibernation, dormice have a restricted breeding season, and only early (in late May–early July) born females have the potential to breed during the summer of their birth. Accumulation of sufficient fat reserves before hibernation is very important for survival of dormice over the winter (Juškaitis 1999b). It could be expected that chances of surviving the winter might be less in breeding young-of-the-year females than in non-breeding females. However, the present study indicates that survival rates of breeding and non-breeding young-of-the-year females from the same cohort did not differ at all.

Why do all early born young-of-the-year females not breed during the summer of their birth? I found that the proportion of breeding young-of-the-year females was inversely related to the spring population density and particularly to the density of adult females. This is one aspect of the density-dependent self-regulation pattern, which was found in the common dormouse populations investigated (Juškaitis 2003). According to Wolff (1997), if self-regulation is to occur, it will be mediated through territoriality and reproductive suppression, which limit the number of breeding females in a population. Adult common dormice were sedentary having a fixed home range of 0.8–1.0 ha through the whole of their active season (Juškaitis 1997b). Male home ranges partially overlapped those of females and each other, whereas female home ranges hardly ever overlapped. Possession of a home range is an indispensable condition for dormouse females breeding. Because of strong territoriality of adult females, breeding by young-of-the-year females may be possible only when population density is low. In such cases, young-of-the-year females would have a greater possibility of finding free territories in which to breed.

Density dependent reproductive suppression is known from many small rodents, but usually only at the highest population densities (e.g. Christian 1971, Pucek *et al.* 1993, Wilson *et al.* 1993, Wolff 1997, Prevot-Julliard *et al.* 1999,

Stenseth *et al.* 2002). In the Białowieża National Park, intrinsic factors acted at outbreak densities of the bank vole (*Clethrionomys glareolus*) and yellow-necked mouse (*Apodemus flavicollis*). However, at moderate densities, the social regulation was easily suppressed under good feeding conditions (Pucek *et al.* 1993). Density-dependent relationships between the maturation rate of young bank voles and the density of already established breeding females was weaker on the food-addition grid (Prevot-Julliard *et al.* 1999). Thus, extrinsic factors such as food level, may also interact with density in determining the proportion of females entering the breeding population.

Prevot-Julliard *et al.* (1999) found that delayed maturation in female bank voles is due to social constraints. This also fits the common dormouse populations investigated: a social system of adult female territoriality causes young-of-the-year females to delay maturation if vacant breeding sites are not available. However, in contrast to the vole examples mentioned above, reproductive suppression in young-of-the-year dormouse females is due to social constraints by adult established females not only at high but even at moderate population densities (about 0.9–1.1 adults ha⁻¹). Thus, it seems that intrinsic regulation in the common dormouse populations is stronger than in Microtine voles or *Apodemus* mice populations. Possibly as a consequence of the strong self-regulation mechanisms, population density of the common dormouse was rather low and stable in both Lithuanian populations investigated (0.5–1.4 adults ha⁻¹; Juškaitis 2003).

Some other small mammals with a low frequency of young-of-the-year breeding females have life history tactics similar to the common dormouse in Lithuania. In the northern deer mouse (*Peromyscus maniculatus*) populations in Canada, females seldom bred during the summer of their birth despite having a breeding season, which appears to be long enough for them to become sexually mature (Teferi & Millar 1993, McAdam & Millar 1999). Neither overwinter survival nor future reproductive success were negatively affected by breeding among young-of-the-year female deer mice. Population densities ranged from 5.3 to 20.6 ind. ha⁻¹ among 20 grid-years (Millar & Teferi 1993), and the

amplitude of the density fluctuations was relatively low.

Lusk and Millar (1989) removed overwintered deer mouse females from a population as soon as young were weaned and found a dramatic breeding response by young-of-the-year females relative to control mice. They concluded that reproductive inhibition of young-of-the-year females was a sex-specific response to the presence of adult females. However, that conclusion was qualified by the fact that the removal of overwintered females reduced overall density on the experimental grid and could have had an indirect effect on food resources available to young-of-the-year mice. Later analogous experiments on the same local population indicated that the earlier conclusion was simplistic (Teferi & Millar 1993). Removal of overwintered females does not necessarily produce a breeding response by young-of-the-year females. The obvious interpretation of these data was that maturation of young-of-the-year females was not a simple response to a single cue (Teferi & Millar 1993). Breeding by young-of-the-year females was associated with longer breeding seasons, increased nestling growth rates and female-biased litters (McAdam & Millar 1999).

Earlier studies on the deer mouse (Terman 1965, 1966 cit. after Christian 1971) show further similarities between deer mouse and the common dormouse populations investigated. According to Christian (1971), relatively low amplitude of the fluctuations in deer mouse populations results from the operation of a highly sensitive density-dependent mechanism that inhibits reproduction. This mechanism includes cessation of reproduction in parous females at relatively low densities and inhibition of maturation among 95% of the females born into a population. Density-dependent inhibition of reproduction may be the single most important mechanism regulating and limiting populations of the *Peromyscus* species, although a high mortality rate may be associated with increased density, too (Christian 1971).

Alpine snow vole (*Chionomys nivalis*) populations also show some similarity to the common dormouse populations investigated in Lithuania. The snow vole is a species with very low turnover: young usually do not reproduce in their year of birth, females produce only two lit-

ters per season, litter size was low and survival was high, particularly so during the winter (on average 45%; Yoccoz & Ims 1999). Snow vole populations in the Alps were very stable: the number of breeding adults at the beginning of the breeding season did not vary by more than two-fold during the course of the study. Observations made on alpine common voles (*Microtus arvalis*) point to the same demographic tactics found in the snow vole: low reproductive rates and high survival rates (Yoccoz & Ims 1999). The stable population sizes observed in the Alps may result in stronger density-dependent selection, and therefore lower investment in reproduction and higher survival (Yoccoz & Ims 1999).

Thus, small mammals belonging to different systematic groups and living in different short-season but stable and predictable environments can have similar life history strategies. Comparable studies from such populations are required in order to draw stronger conclusions about this similarity.

Acknowledgements

I thank Prof. P. A. Morris for revision of the English, S. Büchner for access to his unpublished manuscript, Dr. A. Ulevičius, the editor and anonymous referees for useful comments on an earlier version of the present paper. The Lithuanian State Science and Studies Foundation supported dormouse studies in 2001 (grant No T-507). Lithuanian Bird Ringing Center provided rings for marking dormice.

References

- Bertolino, S., Viano, C. & Currado, I. 2001: Population dynamics, breeding patterns and spatial use of the garden dormouse (*Eliomys quercinus*) in an Alpine habitat. — *J. Zool., London* 253: 513–521.
- Bieher, C. 1998: Population dynamics, sexual activity, and reproduction failure in the fat dormouse (*Myoxus glis*). — *J. Zool., London* 244: 223–229.
- Catzefflis, F. 1984: Etude d'une population de Muscardins (*Muscardinus avellanarius*) lors du repos journalier (Mammalia, Gliridae). — *Rev. Suisse Zool.* 91: 851–860.
- Christian, J. J. 1971: Population density and reproduction efficiency. — *Biol. Reprod.* 4: 248–294.
- Ergon, T., MacKinnon, J. L., Stenseth, N. Ch., Boonstra, R. & Lambin, X. 2001: Mechanisms for delayed density-dependent reproductive traits in field voles, *Microtus agrestis*: the importance of inherited environmental effects. — *Oikos* 95: 185–197.

- Flowerdew, J. R. 1976: Ecological methods. — *Mammal Rev.* 6: 123–159.
- French, N. R., Stoddart, D. M. & Bobek, B. 1975: Patterns of demography in small mammal populations. — In: Golley, F. B., Petruszewicz, K. & Ryszkowski, L. (eds.), *Small mammals: their productivity and population dynamics*: 73–102. Cambridge University Press, Cambridge.
- Juškaitis, R. 1997a: Breeding of the common dormouse (*Muscardinus avellanarius* L.) in Lithuania. — *Natura Croatica* 6: 189–197.
- Juškaitis, R. 1997b: Ranging and movement of the common dormouse *Muscardinus avellanarius* in Lithuania. — *Acta Theriol.* 42: 113–122.
- Juškaitis, R. 1999a: Life tables for the common dormouse *Muscardinus avellanarius* in Lithuania. — *Acta Theriol.* 44: 465–470.
- Juškaitis, R. 1999b: Winter mortality of the common dormouse (*Muscardinus avellanarius*) in Lithuania. — *Folia Zool.* 48: 11–16.
- Juškaitis, R. 2001: Weight changes of the common dormouse (*Muscardinus avellanarius* L.) during the year in Lithuania. — *Trakya University Journal of Scientific Research. Series B* 2(2): 79–83.
- Juškaitis, R. 2002: Spatial distribution of the yellow-necked mouse (*Apodemus flavicollis*) in large forest areas and its relation with seed crop of forest trees. — *Mamm. Biol.* 67: 106–111.
- Juškaitis, R. 2003: Abundance dynamics and reproduction success in the common dormouse, *Muscardinus avellanarius*, populations in Lithuania. — *Folia Zool.* 52. [In press].
- Lambin, X. & Yoccoz, N. G. 2001: Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. — *J. Anim. Ecol.* 70: 191–200.
- Likhachev, G. N. [Лихачев, Г. Н.] 1966: [Breeding of the common dormouse in the south part of the Moscow region]. — *Biulleten' MOIP, Biol.* 71: 32–42. [In Russian].
- Likhachev, G. N. [Лихачев, Г. Н.] 1971: [On biology of the common dormouse]. — *Proceedings of the Prioksko-Terrasnij state reserve* 5: 160–175. [In Russian].
- Lusk, S. J. G. & Millar, J. S. 1989: Reproductive inhibition in a short-season population of *Peromyscus maniculatus*. — *J. Anim. Ecol.* 58: 329–341.
- McAdam, A. G. & Millar, J. S. 1999: Breeding by young-of-the-year female deer mice: Why weight? — *Ecoscience* 6: 400–405.
- Millar, J. S. 2001: On reproduction in lemmings. — *Ecoscience* 8: 145–150.
- Millar, J. S. & Teferi, T. 1993: Winter survival in northern *Peromyscus maniculatus*. — *Can. J. Zool.* 71: 125–129.
- Negus, N. C., Berger, P. J. & Forslund, L. G. 1977: Reproductive strategy of *Microtus montanus*. — *J. Mammal.* 58: 347–353.
- Prevot-Julliard, A.-C., Henttonen, H., Yoccoz, N. G. & Stenseth, N. Ch. 1999: Delayed maturation in female bank voles: optimal decision or social constraint? — *J. Anim. Ecol.* 68: 684–697.
- Pucek, Z., Jędrzejewski, W., Jędrzejewska, B. & Pucek, M. 1993: Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. — *Acta Theriol.* 38: 199–232.
- Schlund, W., Scharfe, F. & Ganzhorn, J. U. 2002: Long-term comparison of food availability and reproduction in the edible dormouse (*Glis glis*). — *Mamm. Biol.* 67: 219–232.
- Slacionenko, J. B. [Сластениченко, Ю. Б.] 1990: [Data on maternal behaviour and postnatal development of the dormouse (*Muscardinus avellanarius* L.)]. — *Investigations on vertebrates zoology. Proceedings of the Zoological institute* 213: 143–151. [In Russian].
- Stenseth, N. S., Viljugrein, H., Jędrzejewski, W., Mysterud, A. & Pucek, Z. 2002: Population dynamics of *Clethrionomys glareolus* and *Apodemus flavicollis*: seasonal components of density dependence and density independence. — *Acta Theriol.* 47 (Suppl. 1): 39–67.
- Storch, G. 1978: Familie Gliridae Thomas, 1987 — Schläfer. — In: Niethammer, J. & Krapp, F. (eds.), *Handbuch der Säugetiere Europas I, Rodentia I*: 201–280. Akademische Verlagsgesellschaft, Wiesbaden.
- Teferi, T. & Millar, J. S. 1993: Early maturation by northern *Peromyscus maniculatus*. — *Can. J. Zool.* 75: 1743–1747.
- Tkadle, E. & Zejda, J. 1995: Precocious breeding in female common voles and its relevance to rodent fluctuations. — *Oikos* 73: 231–236.
- Wilson, W. L., Montgomery, W. I. & Elwood, R. W. 1993: Population regulation in the Wood Mouse *Apodemus sylvaticus* (L.). — *Mammal Rev.* 23: 73–92.
- Wolff, J. O. 1997: Population regulation in mammals: an evolutionary perspective. — *J. Anim. Ecol.* 66: 1–13.
- Yoccoz, N. G. & Ims, R. A. 1999: Demography of small mammals in cold regions: the importance of environmental variability. — *Ecological Bulletins* 47: 137–144.