Ecology of the forest dormouse Dryomys nitedula (Pallas 1778) on the north-western edge of its distributional range

ARTICLE *in* MAMMALIA · JANUARY 2015

Impact Factor: 0.68 · DOI: 10.1515/mammalia-2013-0165

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Ecology of the forest dormouse *Dryomys nitedula* (Pallas 1778) on the north-western edge of its distributional range

Abstract: From 1999 to 2013, a long-term capture-mark-recapture study was carried out in a local population of the forest dormouse, *Dryomys nitedula*, in a mixed forest patch surrounded by unsuitable habitat in Lithuania. Many aspects of this population's ecology are different from those situated elsewhere. In the population, the activity period of *D. nitedula* was the shortest in the entire range (about 4.5 months, late April to early September). Breeding season was early and short, most litters were born in early June, and the average litter size (3.2±1.1 young) was very small. The average densities of the local population were 4.5±1 and 6.7±2.1 ind./10 ha after and before hibernation, respectively. The abundance of the local population was stable, and the sex ratio was approaching 1:1 among adult individuals, except in the first years of the study when abundance was higher than usual and the sex ratio was female-biased. One-year-old dormice comprised about 49% of the population, while 2-, 3-, and 4-year-olds and older accounted for 24%, 14% and 13%, respectively. Maximum life span was 6 years in one female and maximum body weight recorded before hibernation was 57.5 g in an adult male.

Keywords: abundance; breeding; demographic structure; Gliridae; local population.

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Introduction

Dormice (Gliridae) form a distinctive family of rodents (Rodentia) deemed interesting from a variety of viewpoints (hibernation, longevity, low reproduction rate, mostly arboreal style of life) relevant to many different fields of biology (Storch 1978, Airapetyants 1983, Rossolimo et al. 2001, Morris 2003). Among dormouse species, the ecologies of the hazel dormouse *Muscardinus avellanarius* (Linnaeus 1758) and the fat dormouse *Glis glis* (Linnaeus 1766) are rather well investigated (reviewed by Juškaitis 2008 and Kryštufek 2010), but there is a lack of detailed life history data in other dormice species, including the forest dormouse *Dryomys nitedula* (Pallas 1778).

There are many studies on selected aspects of the ecology of *Dryomys nitedula*, especially in the area of the former USSR (reviewed by Airapetyants 1983, Rossolimo et al. 2001), as well as in some other countries (e.g., Kratochvil 1967, Schedl 1968, Kryštufek 1985, Nowakowski and Boratyński 2001, Nowakowski and Godlewska 2006, Duma and Giurgiu 2012, Stubbe et al. 2012, Duma 2013). However, most studies focused on the distribution, habitats, reproduction, and diet of *D. nitedula*, while few studies on population ecology (i.e., population density and structure as well as their dynamics) have been published to date (Golodushko and Padutov 1961, Ściński and Borowski 2006, Markov et al. 2009). Long-term capture-mark-recapture (CMR) studies of populations of *D. nitedula* are totally lacking.

Lithuania is situated in the very north-western corner of the large distributional range of *Dryomys nitedula* (Kryštufek and Vohralik 1994, Batsaikhan et al. 2008; see Figure 1). Only two populations of this species are known in Lithuania, and they are both situated in large forest tracts. Studies supported by Fauna & Flora International in 2001–2002 revealed that the population of *D. nitedula* in one of these forest tracts can be considered a metapopulation, i.e., a system of local populations living in suitable habitat patches, which interact with one another via individuals moving among these local populations (Hanski and Gilpin 1991). The local populations of *D. nitedula* in mixed forest stands are mostly isolated by pure Scots pine stands, which are not suitable for their feeding and breeding activities (Angermann 1963, Juškaitis et al. 2012, Pilāts et al. 2012), but are possibly crossed by dispersing juveniles.

The aim of the present study was to ascertain peculiarities of the population ecology of *Dryomys nitedula* on the north-western edge of its distributional range in comparison to the remaining range.

Figure 1 The distributional range of *Dryomys nitedula* and location of the population studied in Lithuania marked with asterisk (based on Batsaikhan et al. 2008).

Materials and methods

Study area

The dormouse study site was situated in the southern part of the large Kazlų Rūda forest tract (area 58,700 ha) in Kaunas district, central Lithuania (54°58′N, 23°30′E; Figure 1). This part of the forest consists of a mosaic of forest stands that differ in terms of main tree species dominance. The majority of the study site was occupied by Scots pine *Pinus sylvestris* L. dominated stands with Norway spruce *Picea abies* (L.) Karst and the birches *Betula pendula* Roth and *B. pubescens* Ehrh. The remaining parts of the site are characterized by birch dominated stands with aspen *Populus tremula* L., Norway spruce and Scots pine; Norway spruce dominated stands with birch and Scots pine; and black alder *Alnus glutinosa* (L.) Gaertn. dominated stands. Most of the forest stands are about 60 years old. Norway spruce, aged at approximately 40 years, grow in the sub-canopy of most of these forest stands. Solitary pedunculate oak *Quercus robur* L. and small-leaved lime *Tilia cordata* Mill. trees also grow in the area. Rowan *Sorbus aucuparia* L. and glossy buckthorn *Frangula alnus* Mill. are the main understorey species, while hazel *Corylus avellana* L. is absent.

Methods

A pilot study of the *Dryomys nitedula* population was carried out in the period 1999–2000 controlling 20 wooden titmice type nestboxes, which were placed in a line along the edge of a forest compartment and forest road. In April 2001, 63 ordinary wooden bird nestboxes were placed in a grid pattern, each at a distance of 50 m from one another (see schemes in Juškaitis et al. 2012). The old nestboxes arranged in a line were removed in early August 2001. In spring 2003, the grid was expanded to 70 nestboxes spread throughout an area of 13.5 ha. The study area with nestboxes was delimited by a treeless belt situated over a gas pipeline to the east, an overgrowing clear-cut area to the west, a forest road to the north, and a pure Scots pine stand to the south. The internal dimensions of nestboxes used were 12×12×23 cm, and the entrance hole diameter was 35 mm. Most nestboxes were placed in spruce trees at a height of 3–4 m.

All dormice caught in nestboxes were marked with aluminum rings (inner diameter 3.0 mm, height 3.0 mm). The rings were placed on the right hind leg above the ankle. During the entire study period, 120 individuals were marked with rings, and the total number of times that dormice were handled was 535. The weight of all the animals caught were determined using Pesola 100 g spring balances (Pesola AG, Baar, Switzerland) with an accuracy

to 0.5 g. Their age and sex were also recorded. Dormice were considered adults if they had survived at least one hibernation. The age of young in litters was estimated according to the development of external features (Lozan et al. 1990). Nestboxes were controlled regularly during the entire dormouse activity period from late April until early September. From May to August, nestboxes were controlled once a month during the periods 1999 to 2000 and 2004 to 2009, and twice a month during the periods 2001 to 2003 and 2010 to 2013.

The minimum-number-alive method (Krebs 1999) was used to estimate the number of dormice residing in the study site in spring and before hibernation. Spring and summer densities were calculated by dividing the respective numbers of dormice by the study site area, which was 13.5 ha. A boundary strip (Flowerdew 1976, Krebs 1999) was not added to the sides of the area containing nestboxes because this area was surrounded by habitat unsuitable for dormice (see above).

Data were analyzed using the Statistica for Windows ver. 7.0 (StatSoft 2004). Results are presented as means ±SE.

Results and discussion

Activity season

The activity season of *Dryomys nitedula* was very short, lasting only about 4.5 months from late April/early May to late August/early September. At an individual level, the activity season of single dormice did not exceed 4 months. Although the earliest overwintered *D. nitedula* was recorded on 20 April 2002, *D. nitedula* were only found in nestboxes in late April in 4 years during the period 1999–2013. In the remaining 11 years, the first dormice were detected in nestboxes in early May, even though the nestboxes were controlled in late April.

The majority of adults left the nestboxes in late August, and only a few individuals were recorded in early September. The latest record of an adult dormouse was on 8 September 2013. Juveniles tended to remain active a little later than adults, with a number still found in nestboxes at the beginning of September and the latest record being on 13 September 2013.

Along with Tartarstan on the northern edge of the dormouse range, where the activity season also lasts about 4.5 months (Airapetyants 1983), the activity season in Lithuania is the shortest in the entire distributional range of *Dryomys nitedula*. In other parts of the range where the dormice hibernate, the activity season starts a little earlier or at similar time (April to early May), but ends later. In Bialowieza forest, situated on the border of Belarus and Poland about 250 km to the south of the Lithuanian study site, the activity season lasts about 5 months. In the Belorussian part of the Bialowieza forest, *D. nitedula* were found in nestboxes from May to September and left them for hibernation in October (Golodushko and Padutov 1961). Meanwhile, in the Polish part of the same forest, dormice were live-trapped from the beginning of May until the end of September (Ściński and Borowski 2006). In the Voronezh reserve, the last active *D. nitedula* were recorded in late September and early October in two successive years (Angermann 1963).

In the more southerly situated parts of the range, the activity season of *Dryomys nitedula* is even longer. The activity season of *D. nitedula* lasts about 5.5 months (mid-April to early October) in the Czech Republic (Mašková and Adamík 2012), about 6 months (May to October) in the Eastern Alps (Paolucci et al. 1987), about 6.5 months (April to mid-October) in Moldova (Lozan 1970), and 8 months (April to November) in Bulgaria (Markov et al. 2009). In Israel, which marks the southern limit of the distribution range, *D. nitedula* are active throughout the year with short periods of torpor in the winter season (Nevo and Amir 1964).

The length of hibernation is also environmentally driven in other dormouse species. The garden dormice *Eliomys quercinus* L. are obligate hibernators in northern populations, but in the mild climate of Spain, they even shift the reproductive activity to the winter months (Viñals et al. 2012). In some Mediterranean ecosystems, the absence of a hibernation period has also been recorded in hazel dormice, which can be attributed to climatic factors such as mild winters and hot summers (Panchetti et al. 2004).

It remains unclear why *Dryomys nitedula* begins hibernation so early in Lithuania. Two other dormouse species in Lithuania end their activity seasons much later: fat dormouse in late September to early October (with one exceptionally late record on 27 October) and the common dormouse in October to early November (latest record on 9 November) (Juškaitis 2008, 2010; V. Šiožinytė pers. com.).

Breeding

Dryomys nitedula has only one litter of young during the short activity season. During the study period, young were born from late May until the end of June, peaking in early June (Figure 2). The number of young in litters ranged from one to five, with litters of four young being most frequent

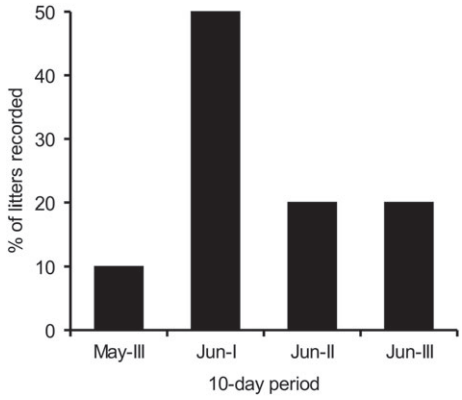

Figure 2 Birth time of young (n=20 litters) of *Dryomys nitedula* in the local population investigated in Lithuania in the period 1999 to 2013.

(48% of all litters recorded; Figure 3). The mean litter size was 3.2±1.1 young (n=25).

The breeding season of *Dryomys nitedula* is related to the beginning and duration of activity season, and there are considerable differences across the distributional range. In the European part of the range, *D. nitedula* only has one litter, but it seems that in the Caucasus and Central Asia, two litters per season occur (reviewed by Rossolimo et al. 2001). In Israel, the breeding season of *D. nitedula* lasts from March to December and dormice have two to three litters per season (Nevo and Amir 1964).

With the studied population of *Dryomys nitedula* having both a rather early and short breeding season, it was also characterized by low average litter size. In more southerly situated parts of the range, the main breeding season starts later, but the average litter size is larger. For example in the Bialowieza forest, most litters of *D. nitedula* are born in the second half of June, with an average litter size of 3.9 young (Golodushko and Padutov 1961). In the Voronezh reserve, the main period of birth is between 11 and 25 of June and the average litter size is 4.0 and 4.1 young in two successive years, respectively (Angermann 1963). An average of 4.7 (two to six) embryos per female were recorded in central Ukraine, and juveniles are often born from May to June (Samarskii and Samarskii 1979).

In the Asian populations of *Dryomys nitedula*, litter sizes are comparatively high: 4.3 (two to seven) in Tadzhikistan, 4.6 (three to six) in Kirgizstan and even 5.7 (three to nine) in Mongolia (Davydov 1984, Rossolimo et al. 2001, Stubbe et al. 2012). Interestingly in Israel, at the southern edge of the range, where *D. nitedula* had the longest breeding season, the recorded litter size was the lowest across the entire range – an average of only 2.6 (one to four) young, with three young being the most frequent litter size (Nevo and Amir 1964). Thus, recorded litter sizes of *D. nitedula* were smaller at both the southern and northern edges of its range (Israel and Lithuania) and highest on the eastern edge of the range (Mongolia).

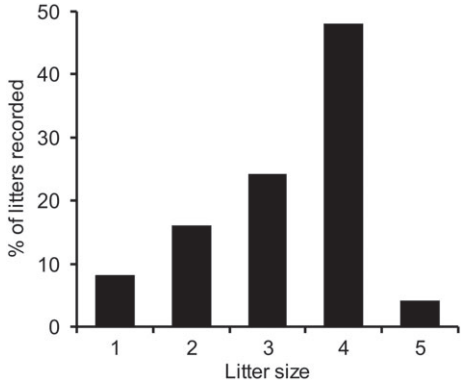

Figure 3 Litter size (n=25) of *Dryomys nitedula* in the local population investigated in Lithuania in the period 1999–2013.

Body weight dynamics

The body weight of adult males and females of *Dryomys nitedula* was rather stable in the period May to July, averaging about 30 g (Figure 4). In August, dormice accumulated fat reserves for hibernation and their body weights increased reaching on average 43 g in late August. The average increase of body weight was 0.4–0.5 g/day, but some individuals managed to increase their weight

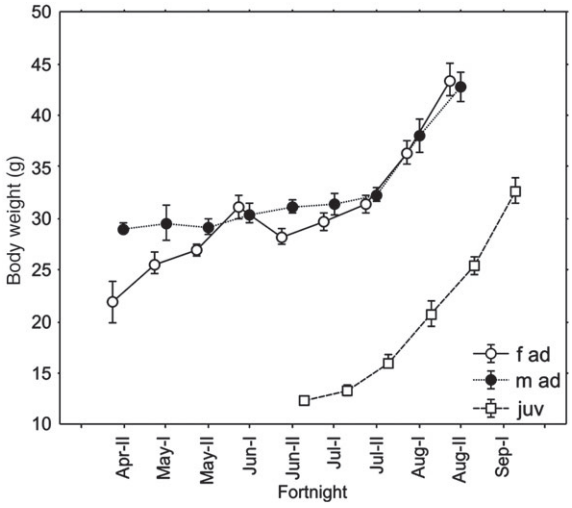

Figure 4 Mean body weight dynamics of *Dryomys nitedula* in adult males (m ad; n=138), adult females (f ad; n=165) and juveniles (juv; n=149) during the activity season in the local population in Lithuania. Pooled data from 1999 to 2013. SE are provided along the mean estimates.

by 1.0–1.4 g/day. In different demographic groups, the maximum body weights recorded were 57.5 g in a 3-year-old male on 25 August 2012, 54.5 g in a 4-year-old female on 8 September 2013 and 43 g in a young-of-the-year female on 1 September 2009.

Published data on body weight dynamics of *Dryomys nitedula* are lacking. To date, the maximum body weight of a European individual before hibernation was recorded in the Voronezh reserve, where an adult male weighing 55.3 g was recorded on 17 September (Angermann 1963). In the Lithuanian population investigated, a higher maximum body weight before hibernation was recorded, which may be related to the longer hibernation period.

It should be noted that even higher body weights for *Dryomys nitedula* were recorded in Mongolia, with maximum body weights of 59 g in males and 48 g in females noted amongst individuals captured in May after hibernation. Mongolian dormice however belong to different subspecies *D. nitedula angelus* (Rossolimo 1971, Stubbe et al. 2012) and it seems individuals of this subspecies are larger than European dormice belonging to subspecies *D. nitedula nitedula*.

Population density

After hibernation, the average population density of *Dryomys nitedula* was 4.5±1.5 adults/10 ha (n=13 years), with a maximum density of 8 adults/10 ha in 2002 and a minimum density of 3 adults/10 ha in 2006 and 2008 to 2010. In August before hibernation, the average population density was 6.7±2.1 ind./10 ha (n=7 years).

The average density of the Lithuanian population is rather similar to estimates obtained in the Polish part of the Bialowieza forest. According to results of a live-trapping study, the density ranged from 1.4 ind./10 ha in June to 18.6 ind./10 ha in September 2003 (Ściński and Borowski 2006). Nowakowski and Boratyński (2001) assessed an average density of *Dryomys nitedula* as 3.3 ind./10 ha (range 1.3–6.9 ind./10 ha) for the whole Polish part of the Bialowieza forest. Taking into consideration only forest stands inhabited by *D. nitedula*, the average density would be ca 6.0 ind./10 ha (range 3.0–10.7 ind./10 ha). Similar densities of *D. nitedula* were also estimated in Central Ukraine: 1–4 ind./10 ha in spring and 3–7 ind./10 ha in summer (Lozan et al. 1990).

Meanwhile, in some more southern parts of the range of *Dryomys nitedula*, ten-fold higher densities were recorded. For example, densities of one to three, eight, and 23 to 25 ind./ha were estimated in three small areas in Moldova (Lozan 1970, Lozan et al. 1990) and a density of 15 to 18 ind./ha in Armenia (Gazaryan 1985, cit. in Rossolimo et al. 2001). The density of the Mongolian population was estimated at about 20 adults/ha after hibernation (Stubbe et al. 2012).

However, it should be noted that in most of the above-mentioned studies (except for the Bialowieza forest), the methods of density estimation are not presented. Thus, these data should be considered as a subjective expert assessment. In several cases, the abundance of *Dryomys nitedula* was estimated as the number of individuals captured in 100 traps/night (Ognev 1947, Rossolimo et al. 2001, Markov et al. 2009). Unfortunately these data are not comparable with density per unit area.

Abundance dynamics

The numbers of adult *Dryomys nitedula* recorded increased at the beginning of the study, reaching a maximum in 2002. From 2003, the numbers decreased by half, thereafter remaining at a similar level for the subsequent 9 years. Some increase in the number of adult dormice recorded was observed in 2012 to 2013 (Figure 5).

According to Rossolimo et al. (2001), pronounced fluctuations in abundance are not typical of populations of *Dryomys nitedula*. The results of our study confirmed this, i.e., the abundance was rather stable during most of the study period. The increased dormouse abundance in the initial stage of the study might be related to the positive influence of a large number of nestboxes placed in the study site. A similar positive effect of nestboxes was recorded in populations of the hazel dormouse (Morris et al. 1990, Juškaitis 2005).

In central Ukraine, however, large fluctuations in *Dryomys nitedula* density were recorded, the numbers varying from 1 to 13 ind./10 ha in different years (Lozan et al. 1990). In this study, however, details on how the authors assessed the densities were not presented. In the Belorussian part of the Bialowieza forest, the abundance of *D. nitedula* was rather stable in spruce-oak-dominated, spruce-dominated and mixed forest stands, but some fluctuations in abundance were observed in young mixed forest stands and pure pine stands over 4 years (Golodushko and Padutov 1961). The authors explained these fluctuations with possible changes in the living conditions in these forest stands.

Sex ratio

The sex ratio amongst adult individuals was different in the first years of the study and later. During most of the

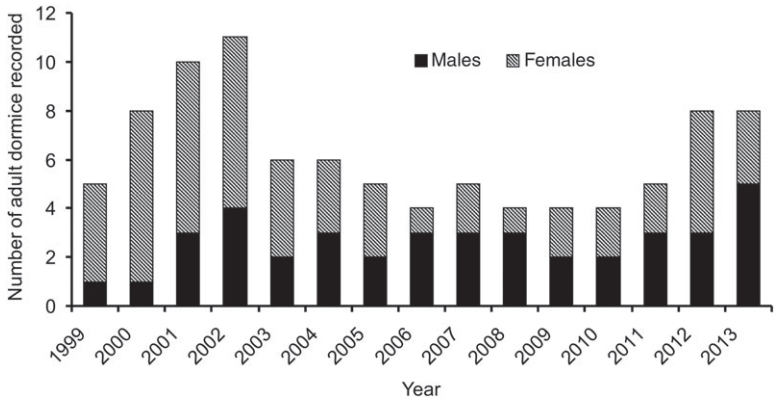

Figure 5 Dynamics of numbers of adult individuals recorded in the local population of *Dryomys nitedula* in Lithuania in the period 1999–2013. Note: only 20 nestboxes arranged in a line were controlled in 1999–2000, whereas 63 nestboxes spread throughout the grid system were controlled in 2001–2002 and 70 nestboxes in 2003–2013.

study period (2003–2013), the sex ratio was close to 1:1 (31 males:28 females), but it was female-biased (73.5%; n=34) during 1999 to 2002 (χ^2=7.53, df=1, p<0.006; Figure 5). In litters (n=22), females (55.4%) prevailed slightly among 74 young recorded.

Published data on the sex ratio in populations of *Dryomys nitedula* are contradictory. In the CMR study carried out by Ściński and Borowski (2006), the sex ratio was not biased (16 males and 16 females), nor was it in Tadzhikistan, where the sex ratio was also close to 1:1 (134 females and 138 males) among *D. nitedula* captured (Davydov 1984). In Bulgaria, however, males (63%) prevailed in the population of *D. nitedula* (Markov et al. 2009).

Females (53.6%) slightly prevailed amongst 151 adult dormice captured in the Belorussian part of the Bialowieza forest, while the sex ratio was 1:1 in juveniles and subadults (Golodushko and Padutov 1961). In the Voronezh reserve, females (56.7 to 65.0%) outnumbered males in all age classes over a period of 2 years (Angermann 1963). In central Ukraine, females accounted for an average of 55.7% amongst 291 dormice captured over a period of 10 years (females prevailed in 8 years, males dominated in 1 year and the sex ratio was 1:1 in 1 year) (Samarskii and Samarskii 1979).

In the Lithuanian population, a female-biased sex ratio was recorded in years when the dormouse abundance increased. When the dormouse abundance decreased, the sex ratio was close to 1:1. Thus, it is possible that the sex ratio may be different in the same population in differing years and may be related to population abundance.

Age structure, life span and survival

On average, when both sexes were pooled, 1-year old dormice accounted for about 49% of all adult individuals recorded, 2-years old 24%, 3-years old 14% and 4- to 6-years old 13%. The age structure of adult males and adult females was rather similar, but slightly increased proportions of 1- and 2-year-olds and lower proportions of 4- to 6-year-olds were recorded in males compared with females (Figure 6).

The maximum lifespan recorded in the *Dryomys nitedula* population investigated was 6 years. Marked as a juvenile on 23 July 2001, one female was last recorded on 23 August 2007, thus surviving more than 6 years in the wild. In total, she was captured 38 times and had 6 litters. One more female and one male survived at least 5 years in the same population.

Out of 80 overwintered *Dryomys nitedula* recorded during 2001 to 2013, 59 individuals were recaptured in the August of the same year. Thus, average summer survival was 73.8% during the study period. Out of 53 adult *D. nitedula* recorded at the study site in August during 2001 to 2012, 38 individuals were recaptured next year

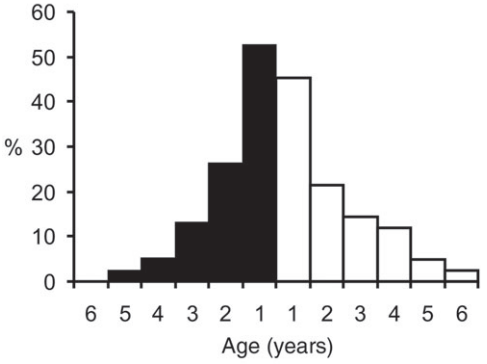

Figure 6 Age structure of adult males (black columns, n=38) and adult females (white columns, n=42) in the local population of *Dryomys nitedula* in Lithuania in 2001–2013.

after hibernation; thus, average winter survival of adult *D. nitedula* was 71.7%.

According to the results of the CMR study carried out in the Bialowieza forest population, 1-year-old (52.6%) and 2-year-old (43.4%) dormice prevailed, while 3-year-old and 4-year-old individuals comprised only 3.6% and 1.2%, respectively (Golodushko and Padutov 1961). The Lithuanian population of *Dryomys nitedula* is distinguished by a much more even age pyramid and higher proportion of older age groups. It should be noted that the age structure pyramid of *D. nitedula* is very similar to analogous age pyramids of the hazel dormouse (Juškaitis 2008).

In several studies, the age structure of *Dryomys nitedula* populations was estimated according to wear of tooth surface, with four age groups identified according to the number of summer seasons survived (Lozan 1961, 1970, Homolka 1979). In this scheme, young-of-the-year dormice and 3-year-old individuals formed the first and fourth age groups, respectively. Markov et al. (2009) found a well-balanced age structure amongst the second, third, and fourth age groups. Meanwhile, Angermann (1963) recorded a high proportion of the second group and a very low proportion of the fourth group. In both cases, dormice older than 3 years were not identified.

According to Lozan (1961, 1970), *Dryomys nitedula* may survive three hibernations and die during the fourth hibernation, i.e., dormice do not reach the age of 4 years. In the CMR study by Golodushko and Padutov (1961), some marked dormice survived up to the age of 4 years. In the Lithuanian CMR study, a maximum life span of at least 6 years was established for *D. nitedula*. This fact is not surprising because the slightly smaller hazel dormice can also survive up to 6 years in the wild (Juškaitis 2008). In captivity, the maximum lifespan of *D. nitedula* was recorded to be a little over 8 years (Airapetyants and Fokin, unpublished).

Conclusions

A local population of *Dryomys nitedula* situated on the north-western edge of the range was found to be distinct from southerly situated European populations of this species in many aspects of its ecology. Differences from Asian populations of *D. nitedula* were even more pronounced. Many extreme indices of dormouse ecology were recorded in the population studied. This population was characterized by the earliest end to the activity season, which also led to one of the shortest durations in the entire range. In turn, the short activity season determined a very short breeding season, again the shortest in the entire range. With the exception of Israel, the average litter size was the lowest in the distribution range. Meanwhile, the highest longevity of *D. nitedula* was recorded in this study, and the population age structure was well balanced. Probably all of these factors compensate for the low reproduction rate.

The shortest activity season determined the longest hibernation period, which lasted about 8 months in this population. Although feeding conditions were not optimal here, dormice managed to accumulate sufficient fat reserves for such a long hibernation period (Juškaitis and Baltrūnaitė 2013). Apart from the Mongolian subspecies of *Dryomys nitedula*, the highest body weight before hibernation was recorded in this population.

A high level of adaptability of *Dryomys nitedula* to local conditions was recorded in previous studies of this population (Juškaitis et al. 2012, Juškaitis and Baltrūnaitė 2013). *D. nitedula* managed to survive in rather poor quality habitats, which have been shown to be incapable of supporting the hazel dormouse (Juškaitis et al. 2012). Elsewhere in the country, hazel dormice were relatively common and widely distributed (Juškaitis 2008), occupying many habitats that should also be suitable for *D. nitedula*. Habitat requirements of these two dormouse species were rather similar and they both lived syntopic in many places elsewhere in their ranges (Juškaitis 2008, Juškaitis et al. 2012). However, *D. nitedula* is very rare in Lithuania and the environmental factors limiting the distribution of *D. nitedula* on the edge of the range are not understood yet.

Acknowledgments: This research was funded by the European Social Fund under the Global Grant measure (Grant No. VP1-3.1-ŠMM-07-K-01-026). Peter Adamík, Vita Šiožinytė, and an anonymous reviewer made valuable comments and suggestions on earlier versions of the manuscript. Linas Balčiauskas and Gintautas Vaitonis helped in the preparation of figures. Jos Stratford revised the English language used in the manuscript.

Received November 15, 2013; accepted February 23, 2014

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