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Summer mortality in the hazel dormouse (*Muscardinus avellanarius*) and its effect on population dynamics

Rimvydas Juškaitis

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Abstract In the period 2000–2012, 38.3 % of 950 marked overwintered hazel dormice (*Muscardinus avellanarius*) were not recaptured at a study site in Lithuania in autumn. As adult dormice are sedentary, it is presumed that those dormice not recaptured died between late April and August. The highest total number of dormice captured for the last time was recorded in May and the lowest in August. The total summer mortality was significantly higher in females (42.5 %) than in males (34.6 %), but it did not depend on dormouse age or body weight. Tawny owl (*Strix aluco*) is the main known dormouse predator in Lithuania, and likely, it has the highest impact on summer mortality of *M. avellanarius*. Over the years, the total summer mortality of adult dormice ranged from 27 % to 52 %. The increased summer mortality resulted in decreased total dormouse population density and particularly decreased density of adult females in summer. Decreased densities led to more intensive breeding in the dormouse population, specifically breeding by young-of-the-year females, a pattern that is not common for this species. The number of breeding cases by young-of-the-year females was inversely related to the density of adult overwintered females in summer and to the number of breeding cases of these females. Breeding by young-of-the-year females was the main factor in the restoration of decreased population density in summer. Lithuanian populations of *M. avellanarius* are unique in their high proportion of breeding cases by young-of-the-year females amongst all populations investigated in the entire species distributional range.

Keywords Common dormouse · Predators · Young-of-the-year females · Breeding · Lithuania

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R. Juškaitis (✉)
Institute of Ecology, Nature Research Centre, Akademijos 2, Vilnius LT-08142, Lithuania
e-mail: juskaitis@ekoi.lt

Introduction

Due to food shortages and adverse weather conditions, winter is a critical period in the life of many small mammals (e.g. Jackson et al. 2001; Merritt et al. 2001; Solonen 2006). For example, winter mortality amounted to an average 77 % of the autumn numbers of bank voles (*Myodes glareolus*) and 86 % of yellow-necked mice (*Apodemus flavicollis*) in Białowieża National Park (Pucek et al. 1993). However, in some populations of small hibernators, survival rates during the overwintering period are much higher than summer survival rates. In five populations of the fat dormouse (*Glis glis*), located over a large geographical range across Europe, the highest survival rate was during hibernation in winter (Lebl et al. 2011). In a garden dormouse (*Eliomys quercinus*) population, the survival rate during hibernation was estimated to be close to unity, whilst the survival rate during the active phase of life in summer was considerably lower (Schaub and Vaterlaus-Schlegel 2001). A similar tendency was also found in adult hazel dormice (*Muscardinus avellanarius*), where monthly survival rates were higher during the hibernation season than the active season (Bieber et al. 2012).

M. avellanarius is a small hibernator, with a hibernation period of up to 7 months. According to its body size (average body weight is 18–20 g in summer and about 30 g in autumn), *M. avellanarius* is similar to other small rodents such as bank voles, yellow-necked mice and wood mice (*Apodemus sylvaticus*), living syntopic in the same forests. However, *M. avellanarius* differs from the abovementioned small rodents significantly in its longevity (a life span of up to 6 years in the wild), low average population density (often only one to three adults/ha) and low reproduction rate (typically only one or two litters per season, the average litter size being four young) (Juškaitis 2008a). Large fluctuations in abundance are typical of populations of voles and mice (e.g. Pucek et al. 1993; Stenseth et al. 2002), whilst in contrast, *M. avellanarius* populations can remain rather stable over long

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periods, even at the northern edge of the range of the species (Juškaitis 2008a).

During earlier capture–mark–recapture studies, it was noticed that many *M. avellanarius* individuals that had been marked and which had survived hibernation, being found in nestboxes in late spring or early summer, were not recaptured later in the course of the active season. Due to low spring population densities, which are typical of dormice populations (Juškaitis 2008a), the disappearance of a portion of the adult reproducing individuals during the breeding season should have significant negative consequences on population abundance.

The aims of the present study are (1) to estimate the mortality rate and to analyse the demographic composition of the *M. avellanarius* which presumably died during late spring and summer and (2) to evaluate the impact of increased summer mortality on population dynamics of *M. avellanarius*.

Material and methods

Investigations into the *M. avellanarius* population were carried out in Šakiai district, south-western Lithuania (55°03'N, 23°04'E) in the period 2000–2012. The dormouse study site covered an area of 60 ha within mixed deciduous–coniferous forest dominated by Norway spruce (*Picea abies*) and birches (*Betula pendula* and *B. pubescens*). The other main tree species growing in the area of the study site were black alder (*Alnus glutinosa*), grey alder (*Alnus incana*), ash (*Fraxinus excelsior*), aspen (*Populus tremula*), small-leaved lime (*Tilia cordata*) and pedunculate oak (*Quercus robur*). Hazel (*Corylus avellana*), glossy buckthorn (*Frangula alnus*), bird cherry (*Padus avium*), rowan (*Sorbus aucuparia*) and dwarf honeysuckle (*Lonicera xylosteum*) were the main species in the understorey. Over most of the study site, the forest was middle-aged (about 60–70 years old). Different forest management operations, including clearfelling, were carried out by foresters (Juškaitis 2008b). In consort with *M. avellanarius*, small mammals belonging to 12 species were recorded in the study site and its surroundings: *Sorex araneus*, *S. minutus*, *Neomys fodiens*, *Apodemus flavicollis*, *A. agrarius*, *Mus musculus*, *Micromys minutus*, *Myodes glareolus*, *Microtus arvalis*, *M. agrestis*, *M. oeconomus* and *M. rossiameridionalis* (R. Juškaitis, unpublished).

Standard wooden nestboxes intended for small hole-nesting birds, e.g. great tit (*Parus major*) and pied flycatcher (*Ficedula hypoleuca*), with internal dimensions of 12 × 12 × 23 cm and an entrance hole diameter of 35 mm were used for the studies of *M. avellanarius*. The boxes were put up at a height of 3–4 m with the entrance facing outwards. In the study site, 272 nestboxes were placed in a grid system at 50 m intervals between boxes. The nestbox density was four boxes per hectare. In the period 2001–2006, 85 additional nestboxes were placed in the north-eastern corner of the study site forming a 25-m nestbox grid.

The nestboxes were controlled during daytime twice a month from April to October. All dormice caught were marked with aluminium rings (inner diameter, 2.5 mm; height, 3.0 mm). The rings were placed on the right hind leg over the ankle. All animals were weighed using PESOLA 100 g spring balances, and their sex and age were determined. Dormice were considered adults if they had survived at least one hibernation. Unmarked young-of-the-year individuals were distinguished from adults by their lower body weight, greyer fur colouration and narrower tail (Juškaitis 2008a).

The minimum number alive method (Krebs 1999) was used to estimate the number of adult dormice living in the area of the study site. Overwintered dormice caught in April, but never recaptured again, were presumed to have died in April; dormice caught in May, but never recaptured again, were presumed to have died in May and so on. However, as dormice also use natural nest sites and some individuals were not recaptured every month during the summer period, the exact month of presumed dormouse death was not known. Recapture probabilities were rather high however (see Discussion).

The total dormouse density and density of adult females were calculated by dividing the number of adult dormice and adult females, respectively, known to be alive in particular periods by the effective trapping area (Flowerdew 1976; Krebs 1999). The trapping area (=68 ha) was calculated by adding a 50-m wide boundary strip to the sides of the area containing nestboxes, except when this area was delimited by forest edge. Breeding females were considered to be not only females found in nestboxes with litters but also those that were caught pregnant or with distinct nipples presumably having litters in natural nests.

The felling of all the understorey consisting mainly of hazel in the area of about 20 ha in 1999 and 2000 had a temporary negative effect on *M. avellanarius* habitat and population density in the years 1999–2002 (Juškaitis 2008b, see also Fig. 2). For this reason, the data from 2000–2002 were excluded from Spearman's rank correlation analysis. To account for multiple tests on repeated data, the level of significance was calculated using Bonferroni correction. Statistical analysis was performed using the STATISTICA 7.0 package (StatSoft 2004).

Results

In the period 2000–2012, out of the total 950 marked overwintered *M. avellanarius*, 364 individuals were not

recaptured in autumn, i.e. after September 1. The highest total number of dormice captured for the last time was recorded in May and the lowest in August, whilst the numbers in April, June and July were quite similar (Table 1). During the entire study period, the proportion of individuals not recaptured was significantly higher in females than in males (chi-square=6.22, p=0.013, df=1). Comparing 1-year-old males with males older than 1 year, the proportions not recaptured were almost equal; the differences between the respective groups of females were also not statistically significant (chi-square=0.87, p=0.35, df=1) (Table 1). Dormice of various ages (from 1 to 6 years old) and body weights (from 10 to 26 g) were amongst those that disappeared from the study site during late spring and summer.

Over the years, the average percentage of overwintered dormice not recaptured in autumn was 38.3±7.5 % and ranged from 27.1 % in 2009 to 51.9 % in 2007. Of note however, the proportions of adult males and females not recaptured in autumn were different in differing years. The proportions of not recaptured adult males (chi-square=4.70, p=0.030, df=1) and females (chi-square=6.60, p=0.010, df=1) in 2000 and 2001 present examples of extreme differences between the sexes (Fig. 1). The highest percentage of not recaptured dormice (more than 50 %) was recorded amongst adult females in 2001, 2004, 2007 and 2011, whilst this figure never reached 50 % in males (Fig. 1).

Dormouse disappearance during the active season determines the decrease in total population density and particularly the density of adult females. In general, across the years, the curves of the dynamics of adult female density after hibernation, as well as adult female density in July, follow the curve of dynamics of total population density in spring (r_s=0.71–0.91, p<0.01, n=13; Fig. 2). However, comparatively high average population densities (1.2 adults/ha) were recorded in spring 2006 and 2007, whilst the densities of adult females decreased considerably in the summer of these years (down to 0.3 female/ha in July). An evident decrease of adult female density was also recorded in summer 2010, whilst the total population density after hibernation in that year was one of the highest during the entire study period (1.4 adults/ha; Fig. 2).

Decreased total population density and particularly a lower density of adult females stimulated more intensive breeding in the population of *M. avellanarius*, which resulted in higher proportions of juveniles in autumnal population. Statistically significant correlations were found between summer densities and the proportions of juveniles in autumn (Table 2). The strongest correlation (r_s=−0.87, p=0.001, n=10) was found between adult female density in July and the proportion of juveniles in population in autumn.

The number of breeding cases by adult overwintered females was positively related to the total population density and to the density of adult females (Table 2). In years when dormouse population density decreased, young-of-the-year females started to breed. The number of breeding cases by young-of-the-year females was inversely related to the summer density of adult females (Table 2) and to the number of breeding cases of adult females (r_s=−0.71, p=0.023, n=10). The highest number of breeding cases by young-of-the-year females was observed in 2006, 2007 and 2011, years in which the lowest adult female density (0.2–0.3 individuals/ha) was recorded in July (Fig. 2).

Discussion

More than one third (38.3 %) of all marked overwintered *M. avellanarius* were not recaptured in autumn. Because adult dormice are sedentary and live in their permanent home ranges (Juškaitis 2008a), it is presumed that these not recaptured dormice died during late April–August. Local survival probabilities are shown to be at their highest during hibernation and lower during the active season in the investigated population (Bieber et al. 2012). Summer recapture

Table 1 Demographic composition of overwintered *M. avellanarius*, which were recorded for the last time at a study site in Lithuania in different months in the period 2000–2012

Month	Females			Males			Total	
	1 year old	>1 year old	Total	1 year old	>1 year old	Total	Number	Percent
April	6	0	6	38	15	53	59	16.2
May	85	17	102	26	24	50	152	41.8
June	27	7	34	21	12	33	67	18.4
July	15	14	29	17	8	25	54	14.8
August	12	5	17	9	6	15	32	8.8
Total	145	43	188	111	65	176	364	100
Summer mortality, %	43.8	38.7	42.5	34.5	34.9	34.6		38.3

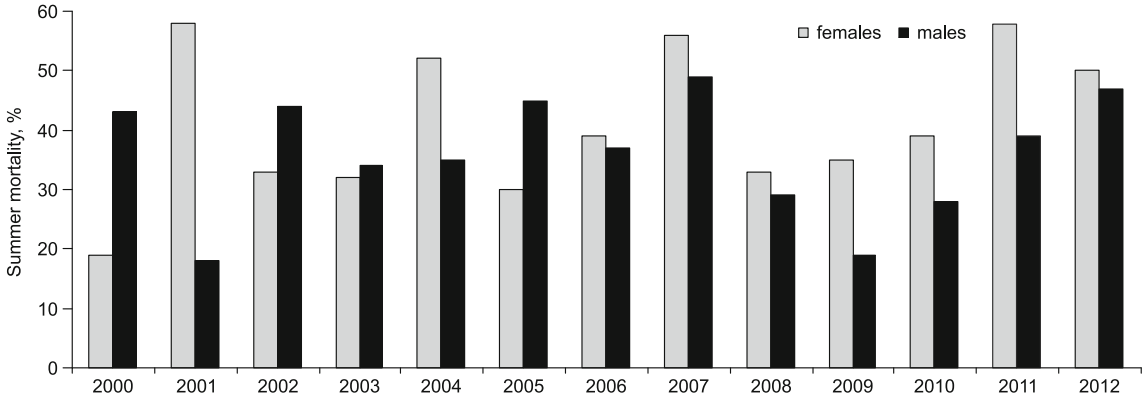

Fig. 1 Dynamics of summer mortality (from mid-April until September) in overwintered males and females *M. avellanarius* at the study site in Lithuania in the period 2000–2012

probabilities of adult *M. avellanarius* evaluated with programme MARK (White and Burnham 1999) were relatively high (0.78 for males and 0.66 for females; C. Bieber, personal communication). Taken together, these data support the assumption that dormice not recaptured during the summer season are likely to have died.

The problem of 'absenteeism' recorded in a British population of the fat dormouse where many marked individuals were absent from nestboxes at a study site for 1 to 3 years before being recaptured again (Morris and Morris 2010) is not characteristic of the *M. avellanarius* population investigated. Over the course of the entire study period, only one individual was recaptured after a year of absenteeism. Additionally, 29 individuals that had not been recaptured in autumn (September–October) were subsequently recaptured the following year. However, adult *M. avellanarius* usually leave nestboxes for hibernation in late September or the first days of October (Juškaitis 2008a); thus, the absence of some individuals from nestboxes during two controls in September is not surprising.

The highest dormouse mortality was recorded in May. Depletion of fat reserves after hibernation and lower food availability may be amongst the reasons for this higher mortality risk for some dormice in late spring (Bieber et al. 2012). However, many *M. avellanarius* in good body condition weighing above 20 g disappeared; thus, it is assumed that predation is the most probable reason of dormouse disappearance.

Throughout the distributional range, the list of predators whose diet includes *M. avellanarius* is rather long, covering 30 species of mammals, birds and reptiles (R. Juškaitis, unpublished). In Lithuania, the tawny owl (*Strix aluco*) is the main known predator of dormice (Balčiauskienė and Balčiauskas 2008), and it is likely to have the highest impact on summer mortality of *M. avellanarius*. Remains of up to four *M. avellanarius* were found in some owl nestboxes after the young had fledged their nests (Juškaitis 2004). Nestlings of tawny owl stay in the nest only for 30–32 days (Mebs and Scherzinger 2000). This means that the dormice whose remains were found in owl nestboxes were hunted by tawny

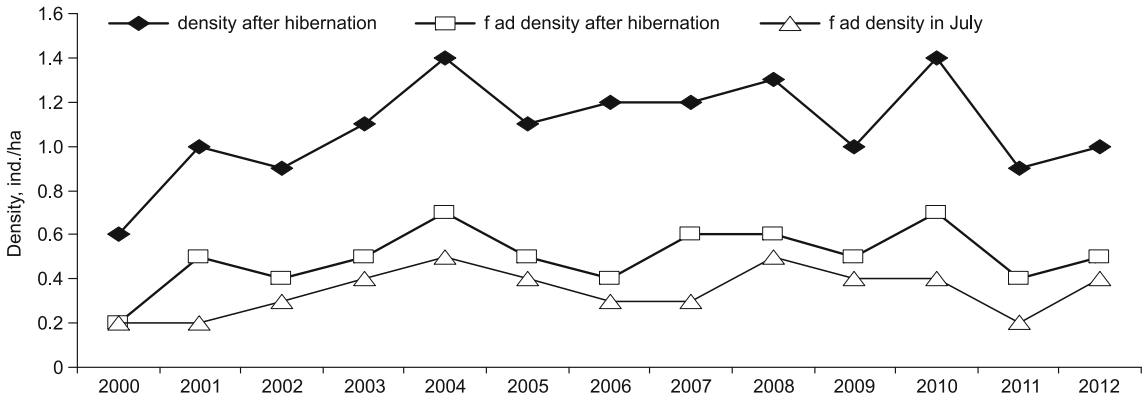

Fig. 2 Dynamics of total population density after hibernation and adult female (f ad) density after hibernation and in July in the population of *M. avellanarius* at the study site in Lithuania in the period 2000–2012. Note: the lower dormouse densities in the period 2000–2002 coincide with recent forest management which negatively affected habitat quality for dormice

Table 2 Spearman's rank correlations between the total population density and adult female density in different months and some breeding parameters at study site in Lithuania in the period 2003–2012

Density, individuals/ha	Breeding parameters		
	Proportion of juveniles in population in autumn (%)	Number of breeding cases by adult females (*n*)	Number of breeding cases by young-of-the-year females (*n*)
Total after hibernation	−0.56	0.59	−0.28
Total in July	−0.81*	0.53	−0.29
Females after hibernation	−0.59	0.67	−0.56
Females in July	−0.87**	0.75*	−0.75*

* $p<0.0125$; ** $p<0.0025$ after Bonferroni correction

owls in just a 1-month period, this period being mainly May in Lithuania (Logminas 1990). Of course, tawny owls could also catch some *M. avellanarius* before and after this period, but the diet of owls outside the breeding period is very little investigated in Lithuania. The decrease in dormouse mortality rate in the latter parts of summer may be related to the increased abundance of other small mammals which are preyed by tawny owls in the study area (Balčiauskienė et al. 2005), thus reducing the likelihood of dormice being preyed upon.

Some other potential predators of *M. avellanarius* also occur in the area of dormouse study site. Evidence of predation by martens (*Martes* spp.) on *M. avellanarius* in nestboxes is present from this area (Juškaitis 2008a and unpublished). Red foxes (*Vulpes vulpes*), wild boars (*Sus scrofa*), least weasels (*Mustela nivalis*) and domestic cats could be other potential predators of *M. avellanarius* in this study site.

Dormouse mortality may also be related with daily torpor, which is typical for *M. avellanarius* in spring. Mostly younger and smaller dormice, whose body weight is less than 15 g, tend to be torpid in spring. In Lithuania, five cases were registered when torpid *M. avellanarius* were found lying on open ground, mostly in early spring (Juškaitis 2008a). Such cases have also been recorded in Britain, Germany and the Czech Republic (P. Morris, B. Schulz, P. Adamík, personal communications). Such torpid dormice lying on open ground can be found and eaten by many mammalian predators or some birds such as corvids (Corvidae). Inclement weather conditions (e.g. heavy rain or long lasting periods of rain) could also affect the survival of dormice, especially of females nursing a litter.

Higher summer mortality amongst adult females of *M. avellanarius* compared to adult males might be related to the reproduction process. Lactating females have increased energetic demands (e.g. Prentice and Prentice 1988; Vaughan et al. 2011); they need more time for foraging during which they are more exposed to predators. Lactating females are even known to leave their nests also in the daytime (Juškaitis 2008a) – a behaviour that might lead to higher risk or mortality.

According to Stenseth and Fagerström (1986), the dynamics of populations of voles (*Myodes* spp.) may, presumably, be entirely understood by only considering females, since a sufficient number of mature males is always available for inseminating mature females in a population. The same assumption may also be applied to *M. avellanarius*, in which populations adult males prevail insignificantly; they are also being more mobile during the mating season (Juškaitis 2008a).

Increased summer mortality had a significant impact on the dormouse breeding pattern in the population studied. The number of breeding cases of adult females was positively correlated with densities of adult females. This means that adult females do not increase their breeding intensity when the population density and the density of adult females have decreased in summer. However, young-of-the-year females start to breed in those years when the population density is low in summer. This phenomenon is significantly related to decreased density of adult females in summer. For example, only a few cases of breeding by young-of-the-year females were recorded in 2012, when the total population density was rather low, but the density of adult females was comparatively high in summer (see Fig. 2). Due to the strong territoriality in adult females, breeding by young-of-the-year females may only be possible when the population density is low. In such cases, young-of-the-year females have a greater possibility of finding free territories in which to breed, whilst adult established females suppress their breeding at moderate population density (Juškaitis 2003).

Breeding by young-of-the-year females is a rather common phenomenon in Lithuania. During 13 years of study, breeding by young-of-the-year females comprised 20.4 % of all breeding cases ($n=515$) recorded in the area of the study site. A very similar proportion of such cases (19.2 %, $n=213$) was recorded at study site B during 1984–1992 (Juškaitis 2008a). However in other parts of the dormouse distributional range, only solitary cases of breeding by females born in the same year were recorded in the Tula and Moscow regions of Russia (Likhachev 1966), Switzerland (Catzeflis 1984), eastern Saxony (Büchner et al. 2003), Romania (Duma 2007), southern England (Eden 2009) and northern Wales (Bird et al. 2012). Thus, amongst all populations investigated in the entire species distributional range, Lithuanian populations of *M. avellanarius* are unique

in their high proportion of breeding cases by young-of-the-year females. Possibly, some geographical differences between populations of *M. avellanarius* exist such as in the case of the fat dormouse when survival rates and breeding patterns of this species were compared across Europe (Lebl et al. 2011). Comparable studies of *M. avellanarius* populations across Europe are necessary to discover these differences.

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