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Dormouse (Gliridae) populations on the northern periphery of their distributional ranges: a review

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Abstract. Geographically peripheral populations are likely to experience suboptimal conditions, and several population characteristics may be influenced. The aim of the present study was to assess characteristics of the populations of hazel, forest and fat dormice on the northern periphery of their ranges in continental Europe in comparison to populations situated in the rest of their ranges. The dormouse populations analysed were found to be distinct from other populations in many aspects of their ecology. On this northern periphery of the ranges, the dormouse activity season is shorter and ends earlier. The population density is also lower, but inter-annual abundance dynamics are comparatively stable. Except the shorter breeding season however, there is no clear general pattern regarding other aspects of reproduction. The composition of the vegetable food used by dormice is rather specific. Contrary to expectations, the proportion of food of animal origin is not increased in the dormouse diets. The main habitat requirements of dormice are similar to those in other parts of their ranges, though the composition of woody plant species in the dormouse habitats is different. Dormice living on the northern periphery of their ranges show a high degree of adaptability to local conditions, but factors limiting their distribution are not clear yet.

Key words: dormice, activity season, breeding, population parameters, diet, habitat selection

Introduction

Geographically peripheral populations are likely to experience suboptimal environment due to less suitable habitats being available, as well as poorer climatic and feeding conditions. At the edge of the distributional range of a species, populations may exist near their limits. Limits on the distribution are mainly posed by climate or its components, resources (food, water or breeding places) or, sometimes, by predators or parasites (Caughley et al. 1988, Avila-Flores et al. 2010, Lloyd et al. 2013). Marginal populations are usually threatened (Lawton 1993), thus knowledge of their ecology is of importance to species conservancy and understanding its ecological niche. For hibernating species, high latitudes with cold climates are extreme. Populations on the northern edge of the species range are called leading edge populations; they survive in the most unfavourable environment and easily become extinct (Hampe & Petit 2005).

Several population characteristics may be influenced at the edge of the geographic range. These include population density (Lawton 1993, Blackburn et al. 1999, Sagarin et al. 2006, Pilāts et al. 2009) and distribution of isolated population within the occurrence area (Lawton 1993, Valdis 2003, Sagarin et al. 2006, Nielsen et al. 2008, Reif et al. 2010), habitat

preferences (Bright 1995, Avila-Flores et al. 2010, Pilāts et al. 2012, Juškaitis et al. 2012, 2013), survival (Caughley et al. 1988, Pitt et al. 2008, Unnsteinsdottir & Hersteinsson 2009), body condition (Carbonell et al. 2003), breeding dates (Millar & McAdam 2001), litter size (Innes & Millar 1987, Ivanter & Kukhareva 2008, Balčiauskas et al. 2012, Stubbe et al. 2012) and reproduction strategy (Vekhnik 2010). Depletion of genetic diversity is also a well-known fact for many species at the edge of their range (Amori et al. 2009, Assis et al. 2013), as are changes in diet composition (Angelstam et al. 1987, Hürner & Michaux 2009, Juškaitis & Baltrūnaitė 2013a, b). For the hibernating species, timing of the activity season is also affected (Ivanter & Kukhareva 2008).

Four dormouse (Gliridae) species – hazel dormouse (*Muscardinus avellanarius*), forest dormouse (*Dryomys nitedula*), fat dormouse (*Glis glis*) and garden dormouse (*Eliomys quercinus*) – have large distributional ranges that extend across Europe and, in the first three species, extend into Asia. The northern distribution limits of *M. avellanarius*, *D. nitedula* and *G. glis* cut through Lithuania, Latvia, Belarus and Russia, while the northern limit of *E. quercinus* reaches Finland, Estonia and the Leningrad region of Russia (IUCN 2014). In Britain, populations of *M.*

avellanarius and *G. glis* also occur on the northern periphery of their ranges, but living conditions are different there due to the maritime climate (Bright & Morris 1996). The aim of the present study was to assess characteristics of populations of *M. avellanarius*, *D. nitedula* and *G. glis* on the northern periphery of their ranges in continental Europe in comparison to populations situated in the rest of their ranges. Unfortunately for unknown reasons, *E. quercinus* has been lost from over half of its former range over the last few decades (IUCN 2014), and analogous comparable data on the ecology of this species are almost absent.

Characteristics of dormouse populations on the northern periphery of their ranges

Activity season

On the northern periphery of the range, the activity season of *M. avellanarius* lasts about seven months. In the Moscow and Tula regions of Russia and in Lithuania, the first overwintered dormice appear in nestboxes in early or mid April (exceptionally in late March). The beginning of dormouse activity season is quite similar throughout the rest of the range. In autumn, *M. avellanarius* leave nestboxes earlier in the northern latitudes than further south. The earliest desertion of nestboxes was recorded in the Tula region, where the last dormouse was found on 10 October (Likhachev 1967a). The situations in Lithuania and the Moscow region are quite similar, with the last dormice being recorded in nestboxes in the beginning of November (Likhachev 1967a, Juškaitis 2014). In southern latitudes and in Britain, considerably higher numbers of dormice are found in boxes in November and even in December, thus the activity season may last over eight months (review in Juškaitis 2014).

Along with Tartarstan (Airapetyants 1983), northern populations of *D. nitedula* have the shortest activity period across the entire range, i.e. only about 4.5 months (late April – early September in Lithuania). Respectively, the hibernation period is very long. Hibernation of *D. nitedula* starts exceptionally early in Lithuania. Adult dormice accumulate fat reserves rapidly during August. They leave nestboxes at the end of August when the weather is still quite warm. Only a few juveniles may be found in nestboxes in early September. In other parts of the range, the activity season starts a little earlier or at similar time (April to early May), but ends much later (October to November, review in Juškaitis 2015).

The activity season of *G. glis* lasts 4-5 months on the northern periphery of the range. *G. glis* were recorded

in nestboxes from late May until mid October in Latvia and during a similar period (second half of May until mid October) in Lithuania (Pilāts et al. 2009, Juškaitis & Augutė 2015). The shortest reported activity season of *G. glis* is that from the Kazan region of Russia: 8 June-25 September (Rossolimo et al. 2001). On the southern edge of the range (central Italy, Sicily), the activity season of *G. glis* may last more than six months (from late April-May until early November-early December, Santini 1978, Milazzo et al. 2003). Thus, for all three dormouse species investigated, it is characteristic that their activity seasons start at a rather similar time across most of their ranges, but the activity seasons finish much earlier in the northern latitudes. Consequently, the dormouse activity season is at its shortest and hibernation at its longest on the northern peripheries of their ranges. It should be noted that the activity season of adult dormice is shorter than that of the entire population: adult *M. avellanarius* are active for only about six months and *G. glis* and *D. nitedula* for only about four months.

Breeding

The shortest breeding seasons of *M. avellanarius* were recorded in the Moscow and Tula regions, where young were born 30 May-9 September and 16 May-2 September respectively (Likhachev 1966). In Lithuania, the timing of birth in *M. avellanarius* is 15 May-22 September. At more southern latitudes where dormice still hibernate, the breeding season starts at a similar time or earlier, but finishes later. For example, in Germany and England, the latest births were recorded in October and in November (exceptionally even in December) respectively (review in Juškaitis 2014).

In the northern populations of *M. avellanarius*, average litter size (4.1 young in Lithuania, 4.3 in the Moscow region and 4.6 in the Tula region) is near to average litter size across the whole range (2.9-5.8 young). Both in Lithuania and in Russia, *M. avellanarius* have two litters regularly as in the rest of the range. In Lithuania, even three litters are possible in exceptional cases, a fact that appears unique across the range. Lithuanian populations of *M. avellanarius* are also unique in their high proportion (18.3 %) of breeding cases by young-of-the-year females, as only exceptionally such cases were recorded in Russia, Switzerland, Germany, Romania and Britain (Juškaitis 2014).

In the north-western corner of the range, the breeding season of *D. nitedula* starts early and is short. Most litters appear in early June and the average litter size

is very small (3.2 young). In more southerly situated parts of the range where dormice hibernate, the breeding season starts a little later and average litter size is larger (3.9-4.7 young, Juškaitis 2015). The largest average litter size – 5.7 young – was recorded in Mongolia (Stubbe et al. 2012). The longest breeding season and the smallest average litter size (2.6 young) is characteristic to Israel, where *D. nitedula* have two to three litters per season (Nevo & Amir 1964). Thus, recorded litter sizes of *D. nitedula* are at their smallest at both the northern and southern edges of its range.

G. glis produces a single litter per year. In Lithuania, the main period of birth is very short – from late July until mid August, although single litters may be born outside this period (Juškaitis & Augutė 2015). In other parts of the range, the birth period may be longer than one month, and in the same localities, newborn and already independent juveniles may be recorded simultaneously (Rossolimo et al. 2001). Average litter size ranges from 4.8 to 6.8 young in different parts of the range (reviews in Rossolimo et al. 2001, Kryštufek 2010). The average litter size of Lithuanian dormice (5.9 young) takes an intermediate position among them (Juškaitis & Augutė 2015).

Summarising, on the northern periphery of their ranges, all three dormouse species have shorter breeding seasons in comparison to southern latitudes. However, there is no clear general pattern regarding other aspects of reproduction.

Body weight before hibernation

Dormice accumulate fat reserves before hibernation, and their body weight increases by approximately 50 percent. The average *M. avellanarius* body weight before hibernation is higher in northern populations (29.7 g in the Moscow region and 31.5 g in Lithuania, Likhachev 1967b, Juškaitis 2014) than in southern parts of the range (27.8 g in Switzerland and 25.4-26.0 g in Germany, Catzefflis 1983, B. Bangura, unpublished). On the northern periphery of the range, body weight increase starts earlier than in Germany and Switzerland (September and October respectively).

Data on the average body weight of *D. nitedula* before hibernation are lacking except in Lithuania, where it reaches 43 g. The maximum body weight of *D. nitedula* recorded in Lithuania (57.5 g) is the highest in Europe, exceeding even the 55.3 g recorded in the Voronezh reserve in Russia (Angermann 1963, Juškaitis 2015). In Mongolia, dormice belonging to subspecies *D. nitedula angelus* are much larger: even after hibernation, average body weight was 45 g in males and 38 g in females (Stubbe et al. 2012).

In Lithuania, the average body weight of adult *G. glis* before hibernation (128 g) is one of the lowest across the range (Juškaitis & Augutė 2015), though a lower body weight (105-114 g) was recorded on the eastern periphery of the range (the Samara region of Russia, Vekhnik 2011). In southerly situated parts of the range, it is much higher and can reach 228 g in Croatia (Grubešić et al. 2004), 192-220 g in Slovenia (Kryštufek & Flajšman 2007) and 167 g in Germany (Fietz et al. 2005).

Summarising, on the northern peripheries, the dormouse species analysed differ in the achieved body weight before hibernation: whilst *M. avellanarius* and *D. nitedula* reach their highest body weights in the northern peripheries, *G. glis* in the same northern areas has one of the smallest body weights across their range. The higher body weights of *M. avellanarius* and *D. nitedula* may be related to the longer duration of hibernation in the northern parts of their ranges (see above), while the lower body weight of *G. glis* might be determined by the smaller body size of these animals on the northern periphery, as was found on the eastern periphery of the range (Vekhnik 2011). Thus, geographical variation of body size in dormice may resemble that in shrews: while some species of genus *Sorex* conform to Bergmann's rule (Ochocińska & Taylor 2003), others and the water shrew (*Neomys fodiens*) do not (Yom-Tov & Yom-Tov 2005, Balčiauskas et al. 2014). Similarly, *G. glis* may be exception to Bergmann's rule.

Population density

The average density of *M. avellanarius* populations is one adult/ha both in Lithuania and in Sweden (Berglund & Persson 2012, Juškaitis 2014), but densities can reach 3.0-6.7 adults/ha in the most favourable habitats in Sweden (Berg & Berg 1999). Similar densities (0.8-1.5 adults/ha) were found in the Moscow and Tula regions of Russia (Likhachev 1954). Considerably higher population densities (up to 5-10 adults/ha) were estimated in populations situated more southerly and in Britain (review in Juškaitis 2014).

Average densities of *D. nitedula* in Lithuania (0.5 adults/ha, Juškaitis 2015) are similar to those in the Polish part of the Białowieża forest (0.3 ind./ha, Nowakowski & Boratyński 2001) and in Central Ukraine (0.1-0.4 adults/ha, Lozan et al. 1990). Meanwhile in Moldova, Armenia and Mongolia, ten-fold higher densities up to 15-25 ind./ha were estimated (Gazaryan 1985, Lozan et al. 1990, Stubbe et al. 2012).

Published data on population densities of *G. glis* in different parts of its range are abundant. Densities

in Lithuania and Latvia (0.8-2.0 and two adults/ha respectively) are evidently among the lowest across the whole range (Pilāts et al. 2009, Juškaitis & Augutė 2015). In central and southern populations, the density of *G. glis* may reach up to 10-50 ind./ha (reviews in Rossolimo et al. 2001, Kryštufek & Flajšman 2007). Thus in general, the densities of dormouse populations on the northern periphery of their ranges are much lower than in southerly parts, especially in *G. glis*. It should be noted that in many publications where high dormouse densities are indicated, the methods of density estimation are not presented. Thus, these data should be considered as a subjective expert assessment and such differences may actually be smaller.

Abundance dynamics

Abrupt inter-annual changes in abundance of *M. avellanarius* were not found in Lithuania or the Moscow region; population abundance changed smoothly, no more than three-fold in any two successive years, and changes that did occur usually lasted for several years (Likhachev 1966, Juškaitis 2014). One particular well-studied Lithuanian population of *M. avellanarius* was extraordinary stable: during the 30-year period, the maximum and minimum densities both in spring and in autumn differed only two-fold. Density-dependent self-regulation works well in this population. Some large inter-annual fluctuations of abundance recorded in other countries may be related to methodological reasons (Juškaitis 2014).

The abundance of a local population of *D. nitedula* studied in Lithuania was also rather stable during most of the 16-year study period (Juškaitis 2015). According to Rossolimo et al. (2001), pronounced fluctuations in abundance are not typical for this species.

In Lithuania, only a single evident increase and single evident decrease of abundance were recorded in a studied population of *G. glis* during a 25-year period; after abrupt decrease of abundance, a gradual restoration of the population lasted four years (Juškaitis & Augutė 2015). In central and southern parts of the range, and in Britain, there is considerable inter-annual variability in population densities related to the skip of reproduction in years when European beech (*Fagus sylvatica*) mast is absent (Kryštufek & Zavodnik 2003, Pilastro et al. 2003, Ruf et al. 2006, Morris & Morris 2010). In Slovenia, the periodicity of peak densities is 1-3 years (Kryštufek 2010).

In spite of comparatively low population density, northern dormouse populations maintain rather stable abundance. While populations of *M. avellanarius* and *D. nitedula* do also not fluctuate markedly in other

parts of the range (Lozan 1970, Rossolimo et al. 2001, Juškaitis 2014), northern populations of *G. glis* are obviously different from the central populations in this respect.

Diet

On the northern periphery of the range, the diet of *M. avellanarius* generally follows the same pattern as in other parts of its range: inflorescences in spring, insects in early summer, soft mast in late summer and autumn and hard mast in autumn (Juškaitis 2014). In the north however, dormice utilise different plant species. The fruits of glossy buckthorn (*Frangula alnus*) are very important to *M. avellanarius* for feeding and accumulation of fat reserves in autumn. The proportion of food of animal origin is high only in early summer (Juškaitis & Baltrūnaitė 2013a).

In Lithuania, due to the scarcity of suitable vegetable and animal food in particular periods, *D. nitedula* is forced to feed on less suitable vegetable food such as female catkins of aspen (*Populus tremula*), seeds of birch (*Betula* spp.) and cones of Norway spruce (*Picea abies*). These items, as well as more calorific foods, such as strobiles of Norway spruce, inflorescences of pedunculate oak (*Quercus robur*) and fruits of glossy buckthorn, have not previously been recorded in the diet of *D. nitedula*. Feeding on such foods are peculiarities of the dormouse diet on the north-western edge of its range (Juškaitis & Baltrūnaitė 2013b).

The diet of *G. glis* on the northern periphery of its range is rather specific due to the absence of beech trees, the mast of which is an excellent food source (Kryštufek 2010). Acorns of pedunculate oak become the main food source in late summer and autumn, and even in spring after hibernation. The high prevalence of acorns, the comparatively high proportion of birch seeds and the low proportion of food of animal origin in the diet, as well as feeding on fruits of glossy buckthorn, are the specific features of feeding by *G. glis* on the northern periphery (Juškaitis et al. 2015). Summarising, the diet of all three dormouse species is rather specific on the northern periphery of their ranges, indicating high adaptability to local conditions. Feeding on fruits of glossy buckthorn, being very important in Lithuania and especially to *M. avellanarius*, has not previously been recorded in any of these species. Contrary to expectations, an increase in the proportion of animal food in the diet was not observed. However, feeding on acorns containing comparatively high amounts of tannins, as well as some less calorific vegetable foods or very small seeds

of birch, indicates that feeding conditions are poorer on the northern periphery of dormouse ranges.

Habitat preferences

A well-developed and diverse understorey is the main habitat requirement of *M. avellanarius* across its range (Juškaitis 2014). In Lithuanian habitats, *M. avellanarius* also prefers sites with a better-developed and interconnected understorey, particularly with a good cover of hazel (*Corylus avellana*) and plentiful bird cherry (*Padus avium*) trees and a high diversity of woody plant species in the understorey and overstorey (Juškaitis & Šiožinytė 2008, Juškaitis et al. 2013). *M. avellanarius* also lives in similar habitats in Latvia (Pilāts 1994). In other parts of the range, different woody plant species are important for habitat selection by *M. avellanarius*. For example in Britain, honeysuckle (*Lonicera periclymenum*) and brambles (*Rubus fruticosus* agg.) are important for *M. avellanarius* in their habitats (Bright & Morris 1990), while in central Italy, the heath tree (*Erica arborea*) is the most important understorey species (Panchetti et al. 2007).

The presence of a shrub layer and dense young trees in the understorey is the main habitat requirement of *D. nitedula*, underlined by the name “shrub dormouse” even being proposed for this species (Likhachev 1972, Airapetyants 1983). In Latvia, *D. nitedula* prefers mature forest stands with a rich shrub layer, especially of hazel, as well as forest edges (Pilāts et al. 2012). In Lithuania, preferred nest sites have a higher density of shrubs and higher numbers of young trees (Juškaitis et al. 2012). Thus, in the very north-western corner of its range, *D. nitedula* retains its main habitat requirement – a well-developed and diverse understorey. However, in Lithuania and Latvia, the species composition of the understorey in the habitats of *D. nitedula* differs from other parts of its range, especially those in Asia, thus showing the high plasticity of the species in this respect.

The principal habitat of *G. glis* is deciduous and mixed woodland with a high proportion of mast seeders – beech or oak trees (Kryštufek 2010). The absence of beech trees is a specific feature of habitats of *G. glis* on the northern periphery of their range, and here *G. glis* prefers mature mixed forest stands with old pedunculate oak trees. Old oak trees grow in nine out of ten localities of *G. glis* known in Lithuania (Juškaitis & Augutė 2015). Also in Latvia, *G. glis* shows clear preference to areas with old-growth oaks having wide canopies (Pilāts et al. 2009). A significant positive correlation was found between indices of nestbox use by *G. glis* and total cover of

oak trees as well as number of coniferous trees in the canopy (Juškaitis & Šiožinytė 2008). Well-connected tree canopies are important for dormouse arboreal movements and protection from predators.

Summarising, on the northern periphery of the ranges, all three dormouse species retain habitat requirements also typical for southerly situated populations, but the composition of woody plant species important for dormice may be completely different.

Conclusions

According to the population characteristics analysed, British populations of *M. avellanarius* and *G. glis*, though also situated on the northern periphery of their ranges, are far more similar to central or even southern populations. Continental populations of *M. avellanarius*, *D. nitedula* and *G. glis* situated on the northern periphery of their ranges show a high degree of adaptability to local conditions. They retain their main habitat requirements, but may live in habitats with completely different woody plant species. Their diet generally follows similar pattern as in other parts of their ranges, but different local plant species may become important in their diet. At the same time however they are constrained to feed on some less calorific or less suitable food items. In spite of this, dormice are able to accumulate sufficient fat reserves for hibernation.

All three dormouse species reviewed are hibernators. On the northern periphery of their ranges, with hibernation starting earlier than in southern latitudes, they have shorter activity seasons and longer hibernation periods. Related to the shorter activity season, the dormouse breeding seasons are also shorter in the northern latitudes. Northern populations of all three dormice species are characterised by lower density, especially in *G. glis*, but their abundance is comparatively stable. These peculiarities are common to all three dormouse species, but there is no general pattern regarding other aspects of reproduction.

Another hibernating species – the northern birch mouse (*Sicista betulina*) – has only a few peculiarities in common with dormice on the northern periphery of its range. The hibernation period is longer in the north, and abundance is lower both on the northern and western peripheries of its range in comparison to central parts of the range (Pucek 1982, Ivanter & Kukhareva 2008). Lower abundance on the periphery of ranges seems to be a general fact for many different species (Millar & McAdam 2001, Guo et al. 2005, Sagarin et al. 2006), but not to all (Blackburn et al. 1999). In contrast to dormice, a high amplitude of

inter-annual fluctuations of abundance (15-25-fold) with long-term deep depressions is characteristic for northern populations of *S. betulina* (Ivanter & Kukhareva 2008). Under conditions of low abundance, patterns of population self-regulation are absent in populations of *S. betulina* (Ivanter & Kukhareva 2008). By contrast, population self-regulation is present in populations of *M. avellanarius* on the northern periphery of the range (Juškaitis 2014). Environmental factors limiting the northern edge of dormouse distributions are not yet known. In Lithuania, *M. avellanarius* and *D. nitedula* live sympatrically and have similar habitat requirements. However, while *M. avellanarius* is widespread and occupies a lot of habitats that also seem suitable for

D. nitedula, the latter species is known from only two localities, and one of these is too poor for the permanent existence of *M. avellanarius* (Juškaitis et al. 2012). Thus, the question of why *D. nitedula* is so rare in Lithuania remains unanswered. As knowledge of the limiting factors is crucial in gaining an understanding of current patterns of species distribution (Carbonell et al. 2003, Gaston 2009), further research needs to be carried out to establish these factors limiting dormouse distribution.

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