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Feeding on the edge: the diet of the hazel dormouse *Muscardinus avellanarius* (Linnaeus 1758) on the northern periphery of its distributional range

Abstract: Although the hazel dormouse *Muscardinus avellanarius* is considered both a highly specialized and a threatened mammal species in Europe, it is relatively common and widespread in Lithuania, situated on the northern periphery of its distributional range. We studied dormouse diet over the entire activity season using microscopic analysis of feces to gain a better understanding of its ecology. Our results confirm that the hazel dormouse is indeed a selective feeder, always showing a preference for the reproductive parts of plants. However, the plant species used by dormice in Lithuania are different from those used in other parts of the dormouse range (e.g., England). In Lithuania, the main dormouse food sources are the inflorescence of willow, oak, and spruce in spring; the berries of honeysuckle, raspberry, and glossy buckthorn in summer; and the berries of glossy buckthorn, oak acorns, and hazelnuts in autumn. Only in early summer, the proportion of food of animal origin is high. The berries of glossy buckthorn are very important to dormouse for feeding and accumulation of fat reserves in autumn. The adaptability of dormice to feed on local plants, as well as the sufficient diversity of food plants in their habitats, allows these animals to be relatively common and widespread on the northern periphery of their range.

Keywords: common dormouse; diet; *Frangula alnus*; Lithuania.

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Introduction

The hazel dormouse *Muscardinus avellanarius* (Linnaeus 1758) is considered a threatened species in Europe. It is included in Annex IV of the Habitat and Species Directive of the European Union and Appendix III of the Bern Convention. *M. avellanarius* is an endangered and red-listed species in many European countries (see the review of Juškaitis 2008). It has been argued that *M. avellanarius* needs habitats containing a high diversity of suitable shrub and tree species to ensure a continuity of food supplies through the changing seasons and that it is critically dependent upon the quality and dispersion of the food resources and the timing of their availability (Bright and Morris 1996).

Lithuania is situated on the northern periphery of the distributional range of *Muscardinus avellanarius*. It would be reasonable to expect that living conditions for this species are suboptimal here in comparison with more southerly situated parts of its range and that the species would be rare in Lithuania. However, with the exception of pure pine forests, *M. avellanarius* is relatively common and widely distributed across almost all of the country, albeit at low average densities of about only 1 adult/ha (Juškaitis 2008). In Britain, where *M. avellanarius* also occurs on the northern periphery of its range, it is considered to be rare and endangered, but in the areas it occurs, the average densities of *M. avellanarius* populations are 2.2–3.5 adults/ha (Bright et al. 2006, Bright and Morris 2008). Thus, the average population densities in suitable habitats in Lithuania are two to three times lower than in suitable habitats in Britain.

In Lithuania, *Muscardinus avellanarius* occupies a wide range of habitats, but as assessed by the average population density, these habitats would seem far from the optimal described for this species (Juškaitis 2007b). One way to evaluate the quality of a habitat for a species is to study its feeding ecology in comparison to other areas that are suitable (Litvaitis 2000). On the one hand, if forests in Lithuania have a similar food quality to other European forests that are considered good habitats for *M. avellanarius*, we should expect (1) the use of the same main resources, with a large use of inflorescences and berries of the same or similar plant species or (2) the use of other resources (e.g., large seeds) with high energy content. On the other hand, if Lithuanian forests are less suitable for *M. avellanarius*, we could predict (3) the use of different food resources that provide less energy to dormice.

There are many publications that contain data on the diet of *Muscardinus avellanarius* (e.g., Holišová 1968, Likhachev 1971, Lukshevich 1981, Airapetyants 1983, Lozan et al. 1990, Müller-Stiess 1996, Vogel 1997, Rossolimo et al. 2001, Sarà and Sarà 2007, Juškaitis 2007a). However, studies that have investigated the diet across the entire activity season have only been carried out in England (Richards et al. 1984, Bright and Morris 1993), a factor that influenced our choice of study aim.

The aim of the present study was to investigate the diet of *Muscardinus avellanarius* in Lithuania on the northern periphery of its range, across the entire activity season, and to ascertain any peculiarities in comparison to similar results from England where the species reaches higher average densities in suitable habitats. This comparison could result in a better insight into the feeding ecology of the species, which would be useful for conservation initiatives.

Materials and methods

Study area

The dormouse study site, referred as a study site A in previous publications (e.g., in Juškaitis 2006, 2008) is situated in Šakiai district, southwest Lithuania (55°03′N, 23°04′E). The study site consists of an area of 60 ha and contains 272 standard wooden nestboxes for small hole-nesting birds spaced in a grid system at 50-m intervals between the boxes. The study site incorporates a typical Lithuanian habitat of *Muscardinus avellanarius*, i.e., mixed deciduous-coniferous forest dominated by birches *Betula pendula* and *Betula pubescens*, as well as Norway spruce *Picea abies*. Other main tree species growing in the area of the study site are ash *Fraxinus excelsior*, black alder *Alnus glutinosa*, aspen *Populus tremula*, and pedunculate oak *Quercus robur*. Hazel *Corylus avellana*, glossy buckthorn *Frangula alnus*, rowan *Sorbus aucuparia*, and bird cherry *Padus avium* are the main understory species.

Methods

The diet of *Muscardinus avellanarius* was studied using a noninvasive method, namely, the analysis of dormouse feces. Samples of feces were collected from nestboxes twice a month over the entire dormouse activity season in 2010 (from early April until late October). During every nestbox control, all feces of *M. avellanarius* found inside or on top of the boxes were collected. All the feces from each nestbox were treated as a separate single sample. Every sample contained droppings left by dormice over the previous 2 weeks, and they could have been left by either single individuals or several individuals. A total of 232 samples were collected over the entire dormouse activity season.

Feces were dried at room temperature and weighed. Depending on the sample size, all droppings or a portion of the droppings (10 droppings on average; range, 2–40 droppings), comprising 11%–100% of the whole sample weight) were selected from every sample and weighed, and slides were prepared (1 dropping=1 slide). Every dropping was placed on glass, soaked with water, and carefully separated with a preparation needle. A total of 2416 slides were prepared and examined under an Olympus CX41 light microscope (Olympus Corporation, Tokyo, Japan) at a magnification of ×40–400.

Food remains were identified by comparison to a reference collection. For this purpose, captive *Muscardinus avellanarius* were fed with various vegetable and animal foods available within the study area. Reference slides were prepared both from feces collected during these feeding experiments and from the fresh potential food samples.

All food remains found in droppings were grouped into five types: food of animal origin, inflorescences, vegetative parts of plants, soft mast (berries), and hard mast (nuts, acorns). Inflorescences and soft mast not identified to the species or genus level were attributed to inflorescence of other deciduous trees and other berries, respectively. Typically, the entire single dropping contained food remains of the same type. Data from analysis of single droppings were recalculated to the entire sample weight. Data from all samples collected during a particular nestbox control were summated, and the proportions of food items identified were expressed as the percentage of dry feces weight.

The breadth of food niche was evaluated by Levin's standardized niche breadth (B_A) according to the five main food groups for every 2-week period (Krebs 1999).

Results

After hibernation, the first *Muscardinus avellanarius* appeared in nestboxes in early April. Judging by their body weight (20.0±0.8 g, n=15), the majority of them still had several grams of fat reserves left. It seems they did not feed immediately after hibernation because despite the fact that dormice were found in the nestboxes, fresh droppings were absent. In early April, only one dropping sample was found, and it contained pollen of black alder. In the second half of April, catkins of willow *Salix* spp. (most probably goat willow *Salix caprea*) dominated the diet of *M. avellanarius* (Table 1).

In May, the diet composition of *Muscardinus avellanarius* was the most diverse of the entire activity season (Table 1). Inflorescences of deciduous trees (mostly willow and oak) constituted more than 60% of dormouse diet in early May, the rest consisting of male strobiles of Norway spruce and vegetative parts of plants and insects (most probably aphids and caterpillars). In the second half of May, the proportions of vegetative parts of plants, inflorescences of oak and insects increased considerably.

In June, the diet of *Muscardinus avellanarius* was distinguished by an increased proportion of insects, the proportion being the highest of the entire activity season (Figure 1). The rest of the dormouse diet was made up of inflorescences of oak in the first half of June and berries of honeysuckle *Lonicera xylosteum* in the second half of the month. *M. avellanarius* also occupied nests of pied flycatchers *Ficedula hypoleuca* in nestboxes and destroyed their eggs.

From July, soft mast dominated the diet of *Muscardinus avellanarius*, making up to 100% in the second half of July and in August (Figure 1). Berries of honeysuckle dominated in the first half of July and raspberries *Rubus idaeus* in the second half of July and first half of August. When the availability of these two berries was over, berries of glossy buckthorn became the major food for the rest of the activity season (Table 1).

During September and October, the composition of dormouse diet was rather stable, with berries of glossy buckthorn forming about two-thirds of the diet and hard mast about one-third (Figure 1). Oak acorns dominated the hard mast as the hazel crop was almost absent in the area of the study site in 2010. Fresh catkins of hazel and insects formed a small proportion of the diet before hibernation. *Muscardinus avellanarius* accumulated fat reserves for hibernation by feeding mainly on berries of glossy buckthorn and acorns of oak.

Food niche breadth of *Muscardinus avellanarius* varied widely during the activity season (B_A=0–0.471). The narrowest niche (B_A=0) was typical for April and from the second part of July until the end of August. It was related to the high abundance of the preferred food type (inflorescences of trees and berries of raspberry or

Months	No. of samples	Food of animal origin		Inflorescences				Vegetative parts	Soft mast				Hard mast	
		Insects	Bird eggs	*Salix* spp.	*Quercus robur*	Other deciduous trees	*Picea abies*		*Lonicera xylosteum*	*Rubus idaeus*	*Frangula alnus*	Other berries	*Quercus robur*	*Corylus avellana*
April-I	1					100.0								
April-II	4			95.2				4.8						
May-I	15	12.6		26.2	11.4	24.3	6.2	19.3						
May-II	15	30.0	3.2	2.0	21.7	1.2	0.4	41.5						
June-I	18	63.9	2.5		27.1	0.7		5.8						
June-II	13	73.7						0.4	23.1			2.8		
July-I	8	21.9							73.4	4.7				
July-II	14							0.8		99.2				
August-I	17									63.5	36.5			
August-II	30	0.7								2.5	96.3			0.5
September-I	23	0.1				1.1					57.3	0.8	40.7	
September-II	25	1.6				2.1					64.1	0.7	31.2	0.3
October-I	35	3.6				0.9					72.1	0.2	23.2	
October-II	14	4.7				7.6					39.9		31.7	16.1

Table 1 Dynamics of diet composition (% of dry feces weight) of *Muscardinus avellanarius* at a study site in Lithuania in 2010.

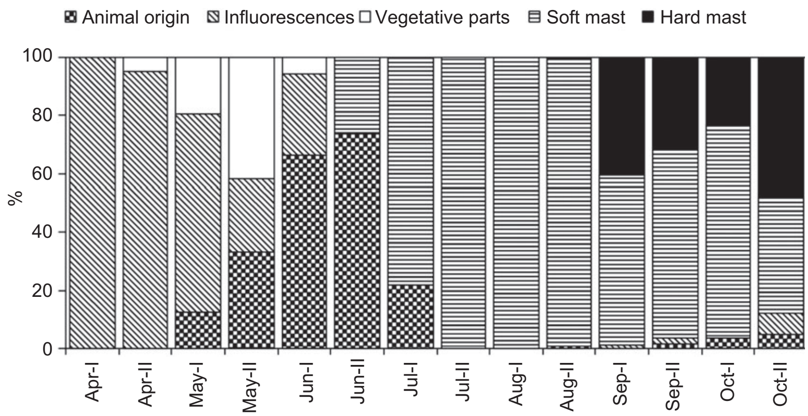

Figure 1 Dynamics of proportions of main food types in the diet of *Muscardinus avellanarius* (% of dry feces weight) in Lithuania during the activity season in 2010.

glossy buckthorn, respectively). The food niche breadth evidently increased in May and in the first half of June (B_A=0.233–0.471), when availability of inflorescences decreased and it was replaced by diverse food (vegetative parts of plants, food of animal origin). The second increase of niche breadth (B_A=0.382) was recorded in late autumn when the diet was mainly composed of hard and soft mast but was also supplemented with catkins of hazel and insects.

Discussion

The analysis of feces is one of the most common methods for the investigation of diet of terrestrial vertebrates (e.g., Litvaitis 2000, Reutter et al. 2005, Nowakowski and Godlewska 2006, Gil-Delgado et al. 2010). Despite its wide use, we have to admit that this technique also has some disadvantages. Because of the differential digestibility of different foods, the proportions of foods eaten and the proportions of food remains in dry feces may be different. Despite this disadvantage, this non-invasive method gives a good qualitative evaluation of animal diet.

In Lithuania, situated on the northern periphery of the distribution range, the diet of *Muscardinus 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 (reviewed by Juškaitis 2007a). In England, only five to seven woody plant species were commonly used by *M. avellanarius* at three study sites (Richards et al. 1984, Bright and Morris 1993). At our study site, the list of potential food plants included about 30 species (Juškaitis 2008), but only seven plant species were of most importance in dormouse diet. Hence, the number of main food plant species is rather similar in both England and Lithuania.

The composition of plant species, however, used by *Muscardinus avellanarius* for feeding is considerably different in Lithuania and England. Only hazel and pedunculate oak are present on the lists of plants used in both countries. Several plant species that are important to *M. avellanarius* for feeding in England (e.g., honeysuckle *Lonicera periclymenum*, bramble *Rubus fruticosus*, hawthorn *Crataegus* spp.) are absent or very rare in Lithuanian dormouse habitats. Some woody plant species important to *M. avellanarius* for feeding in Lithuania, e.g., glossy buckthorn, Norway spruce, raspberry, honeysuckle *Lonicera xylosteum*, are not mentioned in the descriptions of dormouse habitats in England where dormouse feeding was studied (Richards et al. 1984, Bright and Morris 1993). These differences suggest a high adaptability of *M. avellanarius* to local feeding conditions.

In both south Devon (Richards et al. 1984) and Lithuania, insect remains dominated the diet samples in June. This is explained by the scarcity of suitable vegetable food in early summer, when the flowering of most woody plants is over but ripe berries and seeds are still absent. Additionally, insects were found to account for about 8% of total dormouse diet over the entire activity season in Bavarian forests (Müller-Stiess 1996). Eden (2009) suggests that insects may be the major food source of *Muscardinus avellanarius* in some habitats even before hibernation for accumulation of fat reserves. However, it should be noted that the proportion of animal food in the dormouse diet was not higher in Lithuania than in other parts of dormouse range. This indicates that *M. avellanarius* can find sufficient quantities of suitable vegetable food on the periphery of its range.

The consumption of bird eggs by dormice is related to the presence of nestboxes for small hole-nesting birds, where *Muscardinus avellanarius* often occupies the nests of pied flycatchers and some other birds (Juškaitis 2006, Adamík and Král 2008). However, it should be noted that *M. avellanarius* has also been recorded in nests of reed warbler *Acrocephalus scirpaceus* and garden warbler *Sylvia borin*, with the consumption of eggs of garden warbler also recorded by use of a video camera (Berthold and Querner 1986, Honza et al. 1998, Sell 1998).

In our study, vegetative parts of plants comprised 20%–40% of dormouse diet in May. Although dormice (Gliridae) lack a caecum and are less adapted to digesting cellulose using enteric symbionts than other small mammals (Vorontsov 1967), *Muscardinus avellanarius* supplements its diet with easier-to-digest young leaves and buds (Juškaitis 2008, Eden 2009). This is based on observations in captivity, when *M. avellanarius* ate leaf buds of willow and raspberry as well as young leaves of aspen willingly (Juškaitis 2008). Holišová (1968) found remains of leaves of spindle tree *Euonymus verrucosa* by analyzing stomach content, and Richards et al. (1984) found plant epidermis from leaves of honeysuckle *Lonicera periclymenum* by analyzing dormouse feces.

Hazelnuts are considered to be a major food for accumulation of fat reserves before hibernation in *Muscardinus avellanarius* (Bright and Morris 1996). Hazelnut kernels have the highest calorific value (7.9 cal/g dry weight) among European tree seeds that constitute potential food for small mammals (Grodziński and Sawicka-Kapusta 1970). However, the hazel crop was very scarce at our study site in 2010, and this circumstance could influence the smaller total proportion of hard mast in our findings relating to the diet of *M. avellanarius*.

In Lithuania, *Muscardinus avellanarius* has three main food sources for accumulation of fat reserves before hibernation: berries of glossy buckthorn, hazelnuts, and oak acorns. Hazelnuts are the least reliable food source for *M. avellanarius* in autumn: in a 14-year period at our study site, the hazel crop was absent in 4 years, small in 6 years, and only available for dormice to feed upon in September in 4 years (R. Juškaitis, unpublished data). Glossy buckthorn is the most reliable food source for *M. avellanarius* in Lithuania because it fruits almost every year, and this is the most abundant understory species in Lithuanian forests (Navasaitis et al. 2003). Ripe berries of glossy buckthorn are present from late July through November, and they are very important for the accumulation of fat reserves for late-born juveniles in October (Juškaitis 2008).

According to Bright and Morris (1993, 1996), *Muscardinus avellanarius* do not benefit from oak acorns despite their abundance in British woodland. Acorns may be of limited nutritional value to *M. avellanarius* because their high tannin content makes them difficult to digest. If acorns were eaten by *M. avellanarius*, it was perhaps because of scarcity of other food (Bright and Morris 1993). However, notable differences in acorn tannin content, from 2% to nearly 12%, are known to exist among oak species (Shimada and Saitoh 2006). Acorns of the most widespread European oak species, pedunculate oak and sessile oak *Quercus petraea*, are among the most palatable for consumers due to their comparatively low tannin content (5.2%–5.5%) and relatively high metabolizable energy. In all Eastern European publications containing data on feeding by *M. avellanarius*, oak acorns are indicated as a very important component of dormouse diet (e.g., Lozan 1970, Likhachev 1971, Airapetyants 1983). In central Italy and Sicily, oak acorns were also a food resource for *M. avellanarius* in the winter period, during which animals were active (Sarà et al. 2001, Panchetti et al. 2005, Sarà and Sarà 2007).

The results of our study are consistent with the first of our predictions highlighted in the introduction, i.e., Lithuanian dormouse habitats possess food of rather good quality, although the irregular fruiting of hazel and rather high proportion of oak acorns in the autumnal diet of *Muscardinus avellanarius* may indicate that feeding conditions in autumn are a little worse. As mentioned earlier, the average density of *M. avellanarius* populations is two to three times lower in suitable habitats in Lithuania than Britain. Better feeding conditions could have an influence on the higher dormouse densities in Britain, but it seems that food is not a single limiting factor. The density of adult *M. avellanarius* increased by as much as fourfold when nestbox density was increased from 4 to 16 boxes/ha in experimental plot, the feeding conditions being the same in experimental and control plots (Juškaitis 2008). This might suggest that secure nesting sites was the key factor determining dormouse density but not food. The same may be true also for dormouse monitoring sites in Britain where nestboxes are put up in grids spaced about 20 m apart, giving a density of 30 boxes/ha (Bright et al. 2006).

The results of the present study confirm the statement that *Muscardinus avellanarius* is truly a very selective feeder, always showing preference for the reproductive parts of plants (flower buds, inflorescences, berries, and seeds), whereas vegetative parts (leaf buds, leaves, and shoots) are much less favored (Juškaitis 2007a). The adaptability of dormice to feed on local plants, as well as the sufficient naturally occurring diversity of food plants in their habitats, allows these animals to be relatively common and widespread on the northern periphery of their range. The ability of *M. avellanarius* to feed on food of animal origin is also a very adaptive feature, especially in habitats where suitable vegetable food is scarce (Eden 2009).

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