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Feeding in an unpredictable environment: yearly variations in the diet of the hazel dormouse *Muscardinus avellanarius*

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Abstract Yearly variations in the diet composition of the hazel dormouse *Muscardinus avellanarius* were studied in typical dormouse habitat in Lithuania over 5 years (2010–2014) with different feeding conditions. A high proportion of birch seeds in the dormouse diet in two out of 5 years was a very much unexpected result. Dormice consumed them from mid-June until late October even when the most preferable food—hazel nuts—was abundant. In autumn when accumulating fat reserves for hibernation, hazel dormice fed on four main food sources—fruits of glossy buckthorn, oak acorns, hazel nuts and birch seeds. The consumption of these food sources was directly related to their availability. During the study period, only one, two or three of these food sources were abundant in any particular year, while others were absent or scarce. In total, the fruits of glossy buckthorn and oak acorns accounted for the major portion of dormouse diet in autumn. Dormice living in habitat with irregular fruiting of the main food plants are adapted to feed on varying food sources and can switch from one food source to another in different years.

Keywords Common dormouse · Diet composition · Birch seeds · Masting · Lithuania

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Introduction

Dormice (Gliridae) characteristically lack a *caecum* and are less adapted to digest cellulose using enteric symbionts than other small mammals. Due this important trophic limitation, they are less able to exploit easily available foods such as leaves and other green parts of plants. Dormice must concentrate on the most nutritious food sources available, namely, the reproductive parts of plants (flower-buds, flowers, fruits and seeds) or food of animal origin (Bright and Morris 1993, 1996). The presence of highly calorific foods is very important for dormice in autumn when they need to accumulate fat reserves for hibernation (Juškaitis 2014).

The diet of different European dormouse species has been studied intensively during the last decade: in the hazel dormouse *Muscardinus avellanarius* (Juškaitis and Baltrūnaitė 2013a; Chanin et al. 2015), the fat dormouse *Glis glis* (Fietz et al. 2005; Hürner and Michaux 2009; Sailer and Fietz 2009; Vekhnik 2011; Juškaitis et al. 2015), the forest dormouse *Dryomys nitedula* (Magomedov et al. 2012; Juškaitis and Baltrūnaitė 2013b), the garden dormouse *Eliomys quercinus* (Gil-Delgado et al. 2010; Kuipers et al. 2012) and in both fat and forest dormice (Nowakowski and Godlewska 2006; Nowakowski et al. 2006). These studies revealed that food of animal origin accounts for significant portions of the diets of the garden and forest dormice, while hazel and fat dormice are mainly vegetarians, with animal food important for them only in particular seasons, namely, in late spring and early summer. However, their main food plants that supply large calorific seeds—European beach *Fagus sylvatica*, oaks *Quercus* spp. and hazel *Corylus avellana*—do not fruit every year. The response of these two dormouse species to the absence of these food sources is different. In the years when the crop of beech is absent or very scarce, fat dormice may skip reproduction totally and, as a consequence, the abundance of

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their populations can widely fluctuate (e.g. Pilastro et al. 2003; Fietz et al. 2005; Ruf et al. 2006; Lebl et al. 2010; Morris and Morris 2010). Meanwhile, hazel dormice reproduce every year and the abundance of their populations is more stable (review in Juškaitis 2014).

Recently, we investigated the seasonal variability in the diet composition of the hazel dormouse in Lithuania, a territory situated on the northern periphery of the dormouse range. Here, the main dormouse food sources are the inflorescences of willow *Salix* spp., pedunculate oak *Quercus robur* and Norway spruce *Picea abies* in spring; the berries of dwarf honeysuckle *Lonicera xylosteum*, fruits of raspberry *Rubus ideus* and glossy buckthorn *Frangula alnus* in summer; and the fruits of glossy buckthorn, oak acorns and hazel nuts in autumn. Only in early summer, the proportion of food of animal origin is high (Juškaitis and Baltrūnaitė 2013a). However, the hazel and the pedunculate oak do not fruit every year. The fruits of these plants are important for the accumulation of fat reserves for hibernation. The questions arise: what do dormice feed on in the years when the mast of the hazel and pedunculate oak is absent or scarce? What kind of food substitutes them? To answer these questions, we extended our studies on diet composition of the hazel dormouse at the same study site for more 4 years and obtained some unexpected results in years of high mast of birches *Betula* spp.

Material and methods

The dormouse study site is situated in south-west Lithuania, Šakiai district (55°03'N, 23°04'E). The study site occupies 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 the hazel dormouse, i.e., a mixed deciduous-coniferous forest dominated by Norway spruce (30 %), black alder *Alnus glutinosa* (18 %) and birches *Betula pendula* and *Betula pubescens* (17 %). Other major tree species growing at the study site are grey alder *Alnus incana* (9 %), ash *Fraxinus excelsior* (9 %), aspen *Populus tremula* (6 %), small-leaved lime *Tilia cordata* (6 %), willow *Salix* spp. (2 %) and pedunculate oak (2 %). Hazel (30 %), glossy buckthorn (20 %), bird cherry *Padus avium* (19 %), rowan *Sorbus aucuparia* (16 %) and dwarf honeysuckle (13 %) are the main understorey species. The proportions of overstorey and understorey species presented above are based on the evaluation of vegetation parameters around 50 randomly selected nestboxes in the area of the study site (see Juškaitis et al. 2013 for details).

The diet of the hazel dormouse was studied by examining the content of their faeces. The percentage of dry faeces weight was used as the estimation method for diet composition (Litvaitis 2000). Faeces were collected from nestboxes twice a month over the entire dormouse activity season (from early April to late October) in 2010–2014. However, in most cases, faeces were absent in the first half of April despite some dormice being present in the nestboxes. During every routine nestbox inspection, all dormouse faeces found inside or on the top of boxes were collected. They were left by dormice over the previous 2 weeks, and they could have been left by either single dormouse or several individuals. The average number of nestboxes containing dormouse droppings was 16 ± 9 (limits 2–53), and average number of dormice found was 43 ± 34 (limits 3–164) during late April–late October (n = 65 inspections).

Droppings were dried at room temperature. Out of all faeces collected from every nestbox, 2–40 droppings were selected for analysis in 2010, and 5 droppings (less if not available) in 2011–2014. Every dropping was treated as a single sample, and a total of 6349 droppings were analysed (Table S1). Each dropping was weighed with an accuracy to 1 mg, placed on glass, soaked with water, carefully separated with a preparation needles and examined under a microscope at a magnitude of ×40–400. Food remains were identified by comparison to a reference collection obtained from dormouse feeding experiments in captivity and fresh potential food samples. Microscopic analysis enabled us to find microscopic structures typical for every particular food type. All food remains found in droppings were grouped into eight types: bird eggs, insects, inflorescences, vegetative parts of plants, birch seeds, soft mast (soft fruits), hard mast (nuts, acorns) and fungi. Whenever possible, more accurate identification within these types was performed. Typically, single dropping contained only one type of food remains.

The annual variation of masting in pedunculate oak and hazel was evaluated visually on 10–20 trees scattered across the entire area of the study site during inspections of nestboxes in September–October using four categories: absent or almost absent, low, intermediate and abundant (Table 1). Masting of birches was evaluated using the same four categories according to the amount of birch seeds collected by foresters in Lithuania (SFSS 2015). Masting of glossy buckthorn was rather stable during study period.

Table 1 Variation of masting in pedunculate oak, hazel and birches at the study site in Lithuania during 2010–2014. Masting was evaluated using four categories: absent or almost absent (0), low (1), intermediate (2) and abundant (3)

Food plants	Masting in scores in different years				
	2010	2011	2012	2013	2014
Pedunculate oak	1	2	0	3	0
Hazel	0	2	2	1	3
Birches	1	1	3	0	2

Inter-annual differences in the diet were analysed by one-way ANOVA and tested for difference using Tukey's honestly significance difference (HSD) test for unequal sample size. Spearman rank correlation was used to find any relations between the masting of pedunculate oak, hazel and birches and the consumption of oak acorns, hazel nuts and birch seeds during the study period. Statistical analyses were carried out using the STATISTICA 7.0 package (StatSoft, Inc. 2004).

Results

At the beginning of the activity season, dormouse diet composition was rather similar in all 5 years (Fig. 1). Inflorescences of different trees (willow, Norway spruce, pedunculate oak) dominated the diet in the second half of April and in the first half of May. From mid-May until mid-June, inflorescences, vegetative parts of plants and insects (caterpillars and aphids) were the main food sources. The proportions of some particular food items varied depending on their availability in different years (e.g. the presence or absence of inflorescences of Norway spruce, oak acorns or hazel nuts from the previous year).

The high proportion of birch seeds in the diet of the hazel dormouse in two out of the 5 years of the study was the most unexpected result (Fig. 1b). In the years when birch masting was slight, soft mast (fruits of honeysuckle, raspberry and glossy buckthorn) dominated dormouse diet in July and August, and both soft mast (fruits of glossy buckthorn) and hard mast (oak acorns and/or hazel nuts, depending on their availability) in autumn (Fig. 1a). In the years with high masting of birches, birch seeds were present continuously in dormouse diet from mid-June until late October. The proportions of birch seeds varied from 20.6 % even up to 93.8 % in different two-weekly periods (Fig. 1b). The abundant masting of birches influenced the composition of dormouse diet in

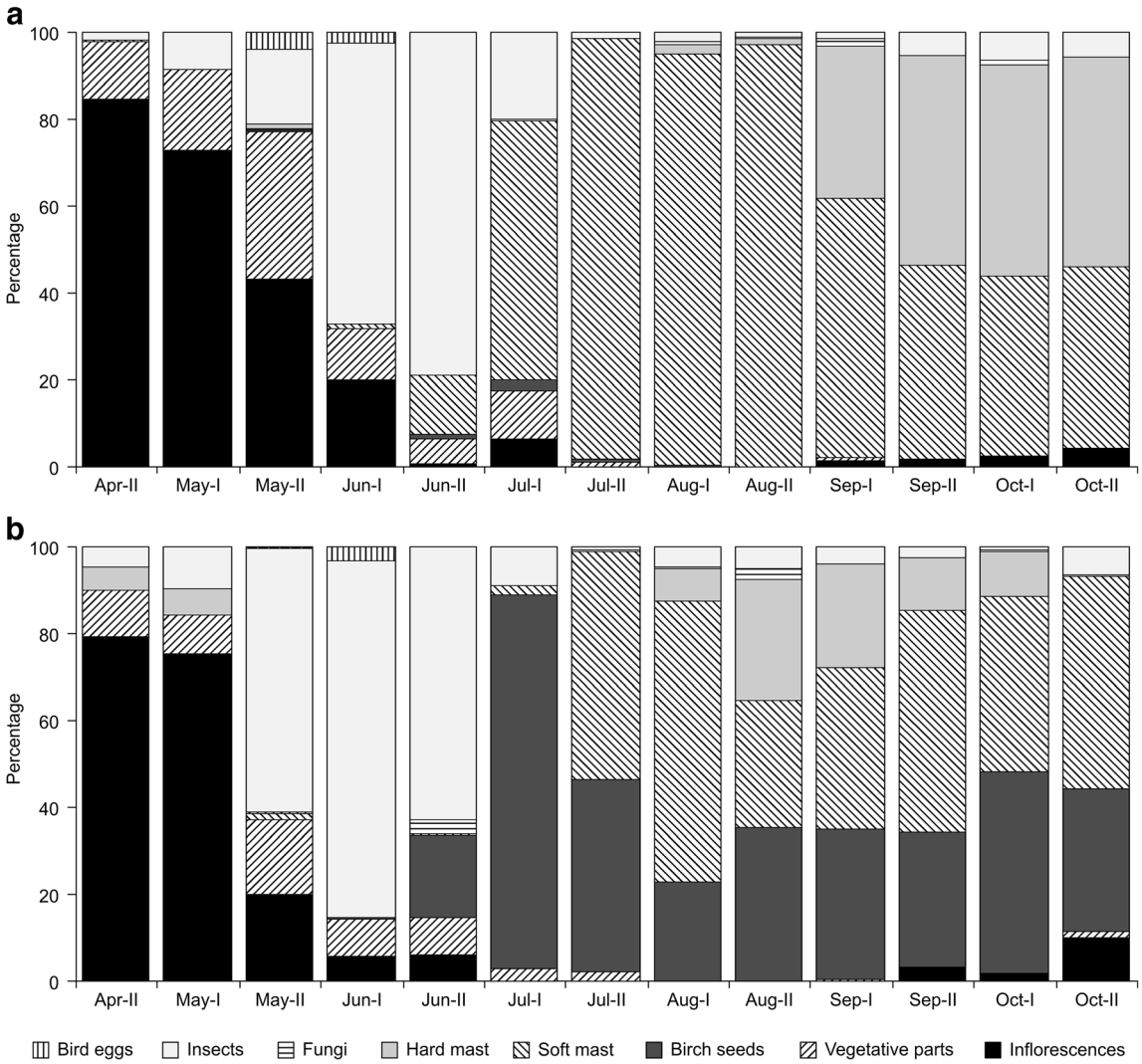

Fig. 1 Seasonal variations in the diet composition of the hazel dormouse (% of dry faeces weight) in mixed forest in Lithuania: **a** when masting of birches *Betula* spp. was low (2010, 2011 and 2013), **b** when masting of birches *Betula* spp. was high (2012 and 2014)

spite of the presence of other preferable food sources. Dormice fed on birch seeds even when the crop of hazel was abundant in 2014.

In autumn when accumulating fat reserves for hibernation, hazel dormice fed on four main food sources: fruits of glossy buckthorn, oak acorns, hazel nuts and birch seeds (Table 2). Usually only two out of these four food sources accounted for the major portion of dormouse diet before hibernation (e.g. glossy buckthorn and oak or glossy buckthorn and birch) because other food sources were absent or scarce. Except the glossy buckthorn, masting of other food plants varied significantly in different years (Table 1). In 3 out of 5 years, the fruits of glossy buckthorn and oak acorns dominated the dormouse diet in autumn. The consumption of oak acorns, hazel nuts and birch seeds during the entire activity season was directly related to their availability, i.e. to the masting of pedunculate oak, hazel and birches (r_S = 0.97, p = 0.005; r_S = 0.97, p = 0.005; r_S = 0.82, p = 0.089, respectively).

The annual consumption of all main food groups varied significantly between years (ANOVA test F = 7.7–255.3, $p < 0.0001$), except in the case of bird eggs (F = 1.3, p = 0.26). The most similar diets were recorded in 2012 and 2014, when no significant difference was found between the diet compositions (HSD test p = 0.25–1.00). The most distinct diets were estimated in 2010 and 2011, when the consumption of all groups was significantly different (HSD test p = 0.003–0.000), except birch seeds (p = 0.93) and bird eggs (p = 0.69).

Apart from the extensive feeding on the seeds of birches, some other new facts on dietary objects of the hazel dormouse were established in the present study. In spring, dormice fed on oak acorns and hazel nuts from the previous year, catkins of hazel and aspen and strobiles of Scots pine *Pinus sylvestris*, while in summer on fruits of wild strawberry *Fragaria vesca* and rowan. In some years, fungi were found in small proportions in the dormouse diet.

Discussion

The value of tree seeds as a food source for forest mammals depends not only on the caloric value of the seeds but also on the seed size, the content of the nutritive material, the palatability, manipulation time and their abundance in a habitat (Grodzinski and Sawicka-Kapusta 1970; Ancillotto et al. 2015). Very small seeds are generally not eaten by voles and mice, but may be regarded as an additional food for shrews, especially in the winter period (Grodzinski and Sawicka-Kapusta 1970). In England, hazel dormice did not forage in trees producing small seeds such as birch, sallow or aspen, at least during the tracking sessions. However, another study demonstrated that dormice may use the seeds of hornbeam and birch, but the handling time required to process such small items may make foraging for them uneconomic (Bright and Morris 1993, 1996).

Seeds of birch are very small, but their caloric value is rather high. The caloric value of whole seeds (including coats) of the white birch (*Betula verucosa* syn. *B. pendula*) is 5.1 kcal/g. This exceeds the caloric value of acorns of pedunculate oak (4.4 kcal/g), but not of the seeds of hazel without shell (7.9 kcal/g) (Grodzinski and Sawicka-Kapusta 1970). However, dormice need much time to open the hard shells of hazel nuts (Eden 2009; Ancillotto et al. 2015); meantime, they eat birch seeds with coats. When birch seeds are abundant in a habitat, it seems dormice do not need much time to collect sufficient amounts of them.

Radio-tracking carried out in England has revealed that hazel dormice do not forage opportunistically, but travel to selected sites and feed on particular resources showing a strong selection for feeding on certain plants that may be rare in surroundings (Bright and Morris 1996). However, it seems that dormice do not behave in such a way when birch seeds are abundant in a habitat regardless of the presence of the more preferable food. Such a situation was observed at the Lithuanian study site in 2014 when the crops of both hazel and birch were abundant: dormice did not prefer hazel nuts, but fed on both hazel nuts and birch seeds.

Distributional ranges of both birch species *B. pendula* and *B. pubescens* cover the major part of Europe (Navasaitis et al. 2003; EUFORGEN 2009) and, except some countries in southern Europe (e.g. Italy, Greece), overlap with ranges of the hazel, fat and forest dormice (IUCN 2015). However, extensive feeding on very small seeds of birches is an unusual phenomenon for dormice, and it has been recorded only in some peripheral populations of the fat dormouse in the Samara region of Russia (Vekhnik 2011) and in Lithuania (Juškaitis et al. 2015), as well as in the peripheral population of the forest dormouse in Lithuania (Juškaitis and Baltrūnaitė 2013b). In the Samara region, feeding on birch seeds by fat

Table 2 Proportions (% of dry faeces weight) of the main components in the diet of the hazel dormouse before hibernation (September–October) in mixed forest in Lithuania in 2010–2014

Year	Fruits of glossy buckthorn	Oak acorns	Hazel nuts	Birch seeds	Other food items
2010	62.0	28.5	2.1	0.0	7.4
2011	37.1	40.7	8.1	0.0	14.1
2012	42.0	0.0	6.0	33.7	18.3
2013	19.0	64.6	1.4	0.0	15.0
2014	25.0	0.3	19.6	39.5	15.6

dormice was recorded in all 4 years of the study, and the frequency of occurrence of birch seeds varied from 30 to 70 % in dormouse diet in different years (Vekhnik 2011). Thus, it seems that on the peripheries of dormouse ranges, the small but abundant seeds of birches may be an important food source for different dormouse species.

For accumulation of fat reserves for hibernation in Lithuania, hazel dormice use four main food sources, out of them only glossy buckthorn has a rather stable fruiting pattern every year. The masting of other main food plants—hazel, pedunculate oak and birches—varies from absent to abundant in different years, but usually at least one or two of them fruit abundantly or moderately in particular year. Dormice living in habitats with such irregular fruiting of the main food plants are adapted to feed on varying food sources. They can switch from one food source to another in different years, and the consumption of these foods is directly related with their availability in the habitat.

However, average dormouse body weight before hibernation varies in different years (R. Juškaitis, unpublished), and this may be related with feeding on different food sources. Lower weight gain and even weight loss were recorded when dormice were fed with oak acorns in captivity (Ancillotto et al. 2015). Acorns may be of limited food value and, as such, woods dominated by tannin-rich acorns could be less suitable for dormice (Bright and Morris 1993, 1996; Ancillotto et al. 2015). Further studies should reveal the importance of different food sources, especially oak acorns and birch seeds, for parameters describing the individual's quality and population structure, such as body mass, survival during hibernation, breeding etc.

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