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Authors: Juškaitis, Rimvydas, and Baltrūnaitė, Laima

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Seasonal variability in the diet of the forest dormouse, *Dryomys nitedula*, on the north-western edge of its distributional range

Rimvydas JUŠKAITIS and Laima BALTRŪNAITĖ

Institute of Ecology of Nature Research Centre, Akademijos 2, LT-08412 Vilnius, Lithuania; e-mail: juskaitis@ekoi.lt

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Abstract. The diet of the forest dormouse, *Dryomys nitedula*, was studied in Lithuania, which is situated on the north-western edge of its range. The diet composition of *D. nitedula* changes constantly over the activity period. From late April until mid-July, food of animal origin dominates the diet, while vegetable food prevails from mid-July until early September. Over the entire activity season, food of animal origin comprises on average 63 % of dormouse diet by volume estimates. Four main food groups – birds, adult insects, insect larvae and millipedes – dominate, but their proportions vary over the course of the season, as does the composition of vegetable food used by *D. nitedula*. Among vegetable food, dormice feed on blossoms of Norway spruce, oak and aspen in May, cones of Norway spruce during June-August, raspberries, birch seeds and fruits of glossy buckthorn in July and August and oak acorns in late August and early September. The composition of vegetable food used by *D. nitedula* in Lithuania is rather specific in comparison to other parts of the range and shows high dormouse adaptability to local conditions. In different years, the proportions of vegetable and animal food, as well as their compositions, vary in the dormouse diet. Dormice can accumulate sufficient fat reserves for hibernation feeding on both vegetable and animal food.

Key words: faecal analysis, birds, insects, millipedes, vegetable food, Lithuania

Introduction

Two dormouse species – the forest dormouse (*Dryomys nitedula*) and the hazel dormouse (*Muscardinus avellanarius*) – are protected by international law under the EU Habitats and Species Directive (Annex IV) and the Bern Convention (Appendix III) in the parts of their ranges where these apply (Amori et al. 2008, Batsaikhan et al. 2008). A lot of attention is paid to the conservation and scientific studies of the hazel dormouse (reviews in Juškaitis 2008, Juškaitis & Büchner 2013), while *D. nitedula* receives significantly less attention in this respect. Only a few studies on the ecology of this species have been carried out in Europe during last decade (e.g. Nowakowski & Godlewska 2006, Ściński & Borowski 2006, Duma & Giurgiu 2012, Juškaitis et al. 2012, Pilāts et al. 2012, Duma 2013).

D. nitedula is distributed over a wider distributional range than any other Palearctic dormouse species. It is found from Switzerland in the west through eastern and southern Europe, Asia Minor and the Caucasus to central Russia and central Asia, reaching as far as 90° E in Mongolia. Many isolated subpopulations occur on the edge of its range, including Israel, central Iran, Afghanistan, the Tien Shan mountains and Sinkiang (China) (Batsaikhan et al. 2008, Stubbe et al. 2012).

Information on food habits is an important introduction to the natural history of any animal species (Litvaitis 2000). A number of authors have studied the food of *D. nitedula* previously, analysing the stomach content of dead animals in different parts of its range (e.g. Ognev 1947, Angermann 1963, Holišová 1968, Davydov 1984, Lozan et al. 1990). However, except of the analysis of faeces conducted by Nowakowski & Godlewska (2006) in Białowieża forest over an entire dormouse activity season, in all other studies the diet was only studied for limited periods of the year or with little detail.

According to published data, vegetable food prevails in the diet of *D. nitedula* in eastern and central parts of its range (Central Asia, the Caucasus), while the proportion of food of animal origin is higher in dormouse diet in northern and western parts of the range (Airapetyants 1983, Rossolimo et al. 2001). Lithuania is situated on the very north-western edge of this large range, and we expected that food of animal

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origin would be even more important for *D. nitedula* here. The aim of the present study was to explore the diet of *D. nitedula* and its seasonal variation on the north-western edge of the dormouse range using a non-invasive method – the microscopic analysis of faecal samples.

Material and Methods

The dormouse study site (area = 13.8 ha) was situated in the southern part of the large Kazlų Rūda forest massive (area 58700 ha) in Kaunas district, central Lithuania (54°58′ N, 23°30′ E). This part of the forest was not homogeneous, with many different small mixed 60 year-old forest stands. The majority of the study site was occupied by Scotch pine (*Pinus sylvestris*) dominated stands with Norway spruce (*Picea abies*) and birches (*Betula pendula* and *B. pubescens*), birch dominated stands with aspen (*Populus tremula*), Norway spruce and Scotch pine, and Norway spruce dominated stands with birch and Scotch pine. A black alder (*Alnus glutinosa*) dominated stand occupied an area of 0.9 ha. Solitary pedunculate oak (*Quercus robur*) and lime (*Tilia cordata*) trees grew in the area of the study site. About 40 year-old Norway spruce trees grew in the sub-canopy of most of these forest stands.

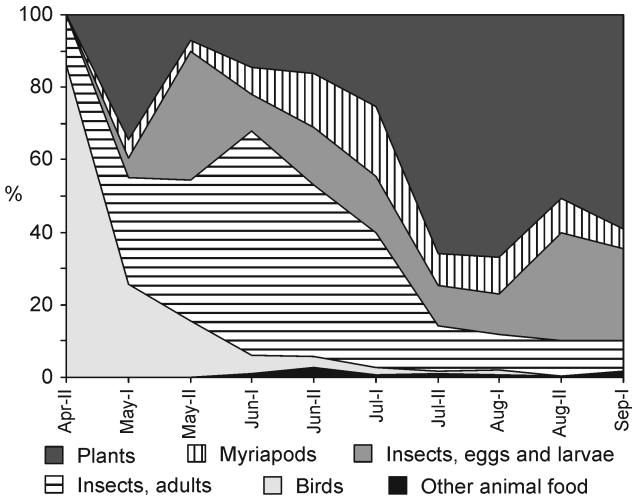


Fig. 1. Dynamics of the percent volume of main food groups in the diet of *D. nitedula* at the study site in Lithuania over the activity season (pooled data from 2010-2012).

Rowan (*Sorbus aucuparia*) and glossy buckthorn (*Frangula alnus*) were the main understorey species. Seventy standard wooden nestboxes for small hole-nesting birds were spaced in a grid system at 50 m intervals between the boxes in the area of the study (see schemes in Juškaitis et al. 2012). Nestboxes were controlled twice every month from late April until

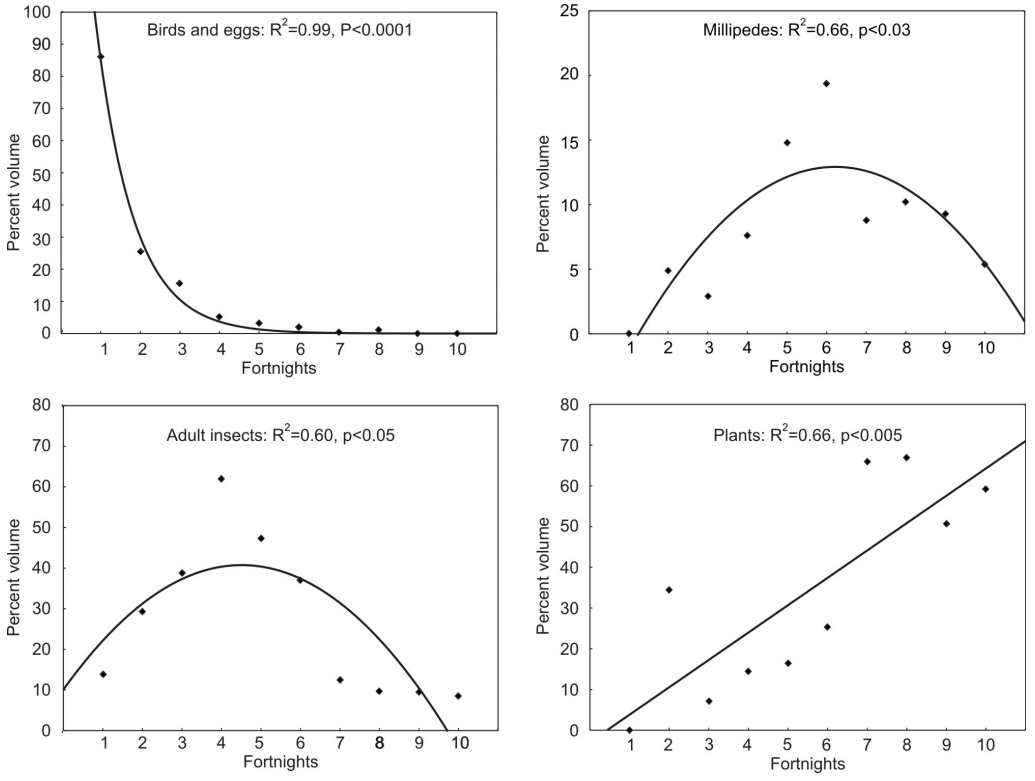


Fig. 2. Regression lines of consumption of four food groups – birds, adult insects, millipedes and plants – by *D. nitedula* in Lithuania over the activity season (pooled data from 2010-2012). Fortnight 1 represents the second half of April, and respectively fortnight 10 is the first half of September.

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Table 1. Diet composition of *D. nitedula* at the study site in Lithuania over the dormouse activity season, expressed in percent as percent volume (V) and frequency of occurrence (FO) (pooled data from 2010-2012).

Food groups	April-II		May-I		May-II		June-I		June-II		July-I		July-II		August-I		August-II		September-I	
	V	FO	V	FO	V	FO	V	FO	V	FO	V	FO	V	FO	V	FO	V	FO	V	FO
Birds	86.2	87.5	22.3	31.6	15.0	20.3	4.9	9.7	3.2	5.3	1.9	3.2	0.6	1.2	1.3	3.1	0.1	0.7		
Bird eggs			3.2	7.0	0.5	1.3	0.2	0.7	< 0.1	0.5	0.1	0.4								
Total Aves	86.2	87.5	25.5	38.0	15.5	20.9	5.1	10.4	3.2	5.8	2.0	3.2	0.6	1.2	1.3	3.1	0.1	0.7		
Myriapoda			4.9	6.3	2.9	5.1	7.6	15.3	14.8	25.2	19.4	34.1	8.8	18.7	10.2	27.4	9.3	18.0	5.4	9.3
Crustacea, Isopoda							0.2	0.7					0.5	2.1	< 0.1	0.6				
Coleoptera	1.3	12.5	16.7	41.8	17.0	50.8	18.0	66.0	8.0	42.2	6.5	31.9	3.1	16.6	1.7	8.8	1.6	10.0	3.6	15.1
Hemiptera, Heteroptera	12.5	12.5	9.1	32.9	3.7	19.3	7.4	29.1	8.6	40.3	7.0	35.5	3.9	27.9	3.7	24.8	2.8	20.0	2.0	8.1
Hemiptera, Homoptera			1.8	3.8	14.8	24.8	31.7	57.8	21.8	38.8	1.7	6.5	0.1	0.6	0.3	1.3	0.2	1.3		
Lepidoptera					0.2	0.6	0.1	0.4	3.4	9.7	12.8	22.2	0.3	1.5	0.3	0.6	0.7	2.0	0.6	1.2
Other insects			1.8	9.5	3.1	18.3	4.7	31.7	5.6	32.5	9.0	41.9	5.1	23.6	3.7	19.5	4.3	18.7	2.3	8.1
Total Insecta, adults	13.8	25.0	29.4	57.6	38.8	68.8	61.9	94.0	47.4	85.4	37.0	77.8	12.5	49.7	9.7	41.5	9.6	36.0	8.5	26.7
Insect eggs							0.9	2.2			< 0.1	0.4	0.4	2.8	< 0.1	0.3	0.7	2.7		
Insect larvae			5.7	20.3	35.4	51.8	9.1	31.7	15.6	40.8	15.6	41.6	10.6	26.7	11.1	31.1	29.2	48.7	25.3	34.9
Total Insecta, eggs and larvae			5.7	20.3	35.5	51.8	10.0	32.8	15.6	40.8	15.6	41.9	11.0	27.9	11.1	31.1	29.9	49.3	25.3	34.9
Arachnida			0.1	0.6	0.1	1.0	0.6	7.5	0.4	5.8	0.6	7.9	0.6	9.5	0.7	10.1	0.4	6.0	1.0	11.6
Mollusca							0.1	0.7	2.2	4.9	0.1	0.4			0.1	0.3			0.6	2.3
Blossoms																				
Picea abies			6.1	10.1	0.5	1.0	0.1	0.4												
Pinus sylvestris					0.6	2.3	0.3	1.5												
Quercus robur			10.0	14.6	0.1	0.3														
Populus tremula			17.9	24.1	3.6	6.8														
Rubus idaeus															0.1	0.6				
Fruits and seeds																				
Betula spp.											9.2	17.2	14.8	33.1	31.8	46.5	27.3	36.7	7.9	11.6
Rubus idaeus											12.2	19.0	43.8	61.7	9.6	20.1	1.1	2.7		
Picea abies			0.4	1.9	2.4	8.0	14.1	35.1	16.4	32.5	3.9	7.9	7.4	12.3	8.2	11.9	0.9	2.7	2.5	5.8
Rubus caesius																	1.2	2.0		
Frangula alnus															17.1	24.5	14.7	28.7	2.6	4.7
Quercus robur																	5.5	8.0	46.2	55.8
Total plants			34.4	50.6	7.2	18.0	14.5	36.9	16.4	32.5	25.3	35.5	66.0	77.9	66.9	82.7	50.7	62.7	59.2	67.4
Number of samples	3		10		24		22		15		16		19		24		13		7	
Number of subsamples	8		158		311		268		206		279		326		318		150		86	

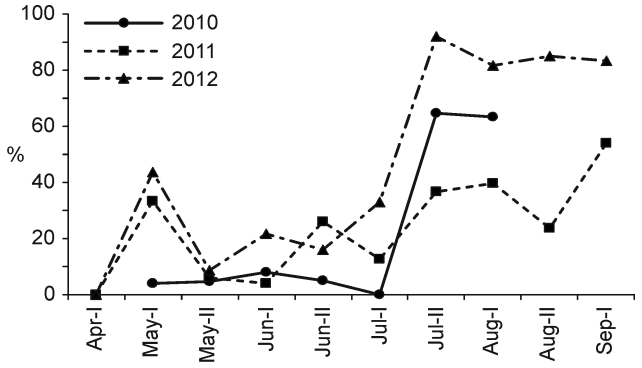


Fig. 3. Dynamics of the percent volume of vegetable food in the diet of *D. nitedula* at the study site in Lithuania over the activity seasons in 2010-2012.

early September, and all faeces of *D. nitedula* found inside or on top of the boxes were collected in 2010-2012. All the faeces from each nestbox were treated as a separate sample. Every sample contained droppings left by dormice over the previous two weeks; they could have been left by either single or several individuals. A total of 153 samples were collected over the entire study period.

Faeces were dried at room temperature and weighed. From every sample, an average of 14 droppings (range 1-40) comprising at least 10 % of the sample weight were selected. Every dropping (treated as a subsample) was soaked in water, placed on glass, carefully separated with preparation needles and analysed under a microscope (at the magnitude × 15-200). A total of 2110 slides were prepared. Food remains were identified through use of a reference collection. For this purpose, potential food items (various insects, millipedes, plants etc.) were collected in the study site and slides were prepared.

All food remains were divided into eight groups: birds (including eggs), millipedes, crustaceans (isopods), adult insects, insect larvae and eggs, arachnids, molluscs and plants. Whenever possible, more accurate identification within these groups was performed. Two estimation methods were applied for diet analysis: 1) the percent volume (V) determined visually within each dropping and 2) frequency of occurrence (FO), i.e. the proportion of droppings containing particular food remains regardless of their volume. A Kruskal-Wallis test was applied to identify seasonal (two-week periods) and inter-annual differences in the consumption of food groups. Linear and non-linear regression analyses were performed to find the best-fitting equations describing consumption of the main food groups during the activity season. Statistical analyses were carried out using the STATISTICA 7.0 package (StatSoft, Inc. 2004).

Results

Food of animal origin comprised on average 63 % V of the diet of *D. nitedula* over the entire activity period, and four main food groups – birds, adult insects, insect larvae and millipedes – dominated (Fig. 1). According to frequency of occurrence, food of animal origin was found in 85 % of faeces of *D. nitedula*, and vegetable food in 51 % of faeces (all months and years pooled together).

Over the entire activity period, the diet composition of *D. nitedula* changed constantly. The consumption of all main food groups differed significantly over the course of the two-week periods (Kruskal-Wallis test by volume, crustaceans: $H = 23.25$, $p < 0.01$, all the rest of the food groups: $H = 40.66\text{-}634.16$, $p < 0.0001$). Feeding on birds and their eggs followed a negative exponential curve (Fig. 2). The consumption of adult insects and millipedes corresponded to a quadratic equation: it increased till mid-summer and then decreased till the end of the activity season. Feeding on plants showed a positive linear increase over the entire activity season. No significant trends were found in consumption of insect larvae and other animal food.

After emerging from hibernation in late April, dormice predated adult hole-nesting birds in nestboxes, primarily on pied flycatchers (*Ficedula hypoleuca*) and great tits (*Parus major*). Dormice consumed all the meat and small bones: only the wings, feathers, legs and parts of the skulls with nibs were usually left. Adult insects were also eaten by dormice in this period. In the first half of May, when blossoms of Norway spruce, oak and aspen were available, they formed an important fraction in dormouse diet (Table 1). Dormice still predated on birds and their eggs, but they also fed on adult insects (Fig. 1).

From late May to early July, food of animal origin dominated dormouse diet, totalling 75-93 % V. In particular, adult insects formed a significant portion of the dormouse diet (37-62 % V), with millipedes and insect larvae also important (the latter especially in the second half of May). Among adult insects, representatives of Coleoptera, Hemiptera and Lepidoptera prevailed (Table 1). The proportion of birds and their eggs decreased significantly in the dormouse diet in this period. Among vegetable food, cones of Norway spruce prevailed in June and raspberries in early July.

From mid-July up to the end of the activity season, vegetable food dominated the dormouse diet, but its composition and proportions of different food items varied. Raspberries dominated among vegetable food

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in late July, but the proportion of birch seeds was also very high during late July to August. In August, dormice also consumed the fruits of glossy buckthorn and acorns of oak (Table 1). The proportion of animal food increased towards the end of the activity season (Fig. 1).

Most adult *D. nitedula* left nestboxes for hibernation in the last days of August, but some young-of-the-year dormice were still active until the 10th September. In early September, the proportions of the main food categories in dormouse diet were similar to those in the second half of August, but oak acorns clearly prevailed among vegetable food (Table 1).

The annual consumption of main food groups varied significantly between years from 2010 to 2012. For example using the Kruskal-Wallis test by volume, birds ($H = 6.22$, $p < 0.05$), arachnids ($H = 7.28$, $p < 0.05$), molluscs ($H = 15.9$, $p < 0.001$), adult insects (18.02, $p < 0.001$), millipedes ($H = 44.19$, $p < 0.0001$), larvae and eggs of insects ($H = 85.3$, $p < 0.0001$) and plants ($H = 106.74$, $p < 0.0001$) all differed significantly. Only crustaceans did not ($H = 0.93$, $p < 0.7$).

In the three years, the total proportion of vegetable food (32 %, 25 % and 46 % V, respectively) and its composition also differed in dormouse diet. The years 2010 and 2012 were similar in the high proportion of vegetable food consumed in the second half of the summer, while in 2011 vegetable food made up only 24-40 % V in this period (Fig. 3). In Lithuania, *D. nitedula* prepare for hibernation accumulating fat reserves in August, and they can increase their body weight by up to 1 g/day in this period (Juškaitis R., unpublished data). Dormice can accumulate sufficient fat reserves feeding on both vegetable food and food of animal origin. In August 2010 and 2012, dormice fed mainly on vegetable food (birch seeds, raspberries, fruits of glossy buckthorn), while in August 2011, food of animal origin (adult insects, insect larvae and millipedes) dominated dormouse diet, but was also supplemented by oak acorns.

Discussion

The frequency of occurrence of different food items is one of the most common evaluation methods in diet analysis of small mammals and, as such, has also been used in recent studies on the diet of dormice (e.g. Nowakowski & Godlewska 2006, Hürner & Michaux 2009, Gil-Delgado et al. 2010, Kuipers et al. 2012). However, in the opinion of Hansson (1970), the frequency of occurrence should only be used for comparisons, e.g. between sexes, seasons, habitats, or species. The danger with these estimates is obvious from the example of wood mouse (*Apodemus sylvaticus*) in England. Based on frequency of occurrence estimates, wood mice were considered to largely live on insects. Analysing this food item by volume estimates however revealed that insects actually made up only a small part of the diet of the species. For this reasons, although they are subjective, volume estimates are more applicable in animal diet analysis and have an obvious biological meaning (Hansson 1970). Ideally, food habits should be expressed both as percent frequency and percent volume (or mass) to facilitate comparisons with other studies. Expressing food habits by percent volume appears to be approximately comparable to the percent mass of different insects consumed (Kunz & Whitaker 1983).

Dormice (Gliridae) lack a *caecum* and are less adapted to digest cellulose using enteric symbionts than other small mammals (Vorontsov 1967). This is an important trophic limitation, due to which dormice 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 fruits of plants or food of animal origin (Airapetyants 1983).

In most published data on the diet of *D. nitedula*, dormouse food is not quantified and only the proportions or numbers of stomachs in which vegetable food and food of animal origin was found are presented. Vegetable food prevails in the diet of *D. nitedula* in places where orchards are present or wild fruiting trees are abundant. The highest proportion of vegetable food was found in Tadzhikistan, where among more than 250 stomachs investigated 74 % of them contained only vegetable food, mostly pulp of apricots, but also fruits of other trees and shrubs belonging to about 20 species (Davydov 1984). Vegetable food (apricots, apples, pears, plums, oak acorns, beech nuts etc.) also dominated the diet of *D. nitedula* in the Caucasus and Moldova, where different fruit trees were abundant (Lozan 1970, Airapetyants 1983, Rossolimo et al. 2001). In environs of Alma-Ata (Kazakhstan), vegetable food was found in 59 stomachs and remains of insects in 58 stomachs in mid-June to August, but apples clearly dominated among stomach content (Ognev 1947).

In northern and western parts of the distribution range of *D. nitedula*, where large orchards and fruiting trees are less abundant, food of animal origin becomes more important in dormouse diet. According to the frequency of occurrence, food of animal origin accounted for 59 % of diet in Ukraine (Lozan et al.

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1990) and 84 % in the Voronezh region of Russia (Angermann 1963). Animal and vegetable food was found in 91 % and 77 % of stomachs respectively in the Volga-Kama region of Russia (Rossolimo et al. 2001) and 100 % and 56 % respectively in Slovakia (Holišová 1968).

Remains of animal food were found in 100 % of faecal samples of *D. nitedula* in Białowieża forest (Poland), while the percentage of faecal samples containing vegetable food (seeds and plant fibres) was rather low (Nowakowski & Godlewska 2006). However in the Belarusian part of Białowieża forest, vegetable food was dominant in the diet of *D. nitedula*, although food of animal origin was also constantly present in rather large quantities and it was vital for dormice (Golodushko & Padutov 1961). Unfortunately, quantifiable data are not presented in this study.

In Lithuania, food of animal origin was found in 85 % of faeces of *D. nitedula*. Thus, the frequency of occurrence of animal food in the diet of *D. nitedula* is lower than in Białowieża forest, Slovakia and the Volga-Kama region of Russia (Holišová 1968, Rossolimo et al. 2001, Nowakowski & Godlewska 2006). This means that the importance of animal food for *D. nitedula* is not greater on the north-western periphery of the range as was expected. It should also be noted that the proportion of animal food in the diet of the hazel dormouse (*Muscardinus avellanarius*) was not higher in Lithuania than in other parts of its range (Juškaitis & Baltrūnaitė 2013). This indicates that both dormouse species can find sufficient quantities of suitable vegetable food on the northern periphery of their ranges.

Seasonal variation in the diet of *D. nitedula* is well expressed both in Lithuania and in other parts of the range, and it is related to the availability of particular suitable foods. In spring and early summer, predation on birds nesting in nestboxes was recorded in the Voronezh region, Białowieża forest, the Czech Republic and Lithuania (Golodushko & Padutov 1961, Angermann 1963, Juškaitis 2006, Nowakowski & Godlewska 2006, Adamík & Král 2008). Dormice kill and eat adult birds and fledglings as well as destroy bird eggs. *D. nitedula* have also been shown to predate on birds nesting in natural cavities, namely on pied flycatchers, collared flycatchers (*Ficedula albicollis*), marsh tits (*Parus palustris*) and blue tits (*Cyanistes caeruleus*) (Walankiewicz 2002, Wesołowski 2002, Czeszczewik & Walankiewicz 2003, Wesołowski & Rowiński 2012).

Feeding on adult insects is recorded in all studies on the diet of *D. nitedula*. Beetles (*Melolontha*, *Geotrupes*), moths and representatives of Hemiptera were most often identified among food remains of *D. nitedula* (Ognev 1947, Golodushko & Padutov 1961, Angermann 1963, Lozan et al. 1990, present study). In Lithuania, adult insects were found in the dormouse diet over the entire activity season, but the highest proportions were recorded before mid-July, prior to the ripening of berries.

Captive dormice willingly ate insect larvae and chrysalises (Angermann 1963, Schedl 1968, Airapetyants 1983). However, probably due to methodological reasons, they were not found in the previous stomach and faecal analysis mentioned above, except the study by Holišová (1968). In Lithuania though, insect larvae formed a significant portion of dormouse diet, especially in the second half of May and before hibernation.

In Lithuania, millipedes constituted a significant portion of the diet of *D. nitedula* over almost the entire activity season. A similar situation was also recorded in Białowieża forest (Nowakowski & Godlewska 2006). Millipedes were also found in dormouse stomach contents in Slovakia (Holišová 1968). However, millipedes are not even mentioned in any other studies on the diet of *D. nitedula* including Ukraine where many species of invertebrates were identified in stomach contents (Lozan et al. 1990). As the remains of millipedes are easily recognisable in dormouse faeces according to the typically numerous body segments with legs (the same should be applied also for stomach contents), it could be concluded that *D. nitedula* feeds on millipedes only in the north-western part of the range. Millipedes and other invertebrates were the staple food of the garden dormouse (*Eliomys quercinus*) in the Netherlands over the entire activity period (Kuipers et al. 2012), as well as in Slovakia (Holišová 1968).

Food of animal origin is important and vital for *D. nitedula*. In the experiment by Golodushko & Padutov (1961), when dormice were fed only with vegetable food, animals started to show signs of ill-health and became less active after 5-7 days. One female even ate her young after not receiving any animal food for 10 days (Golodushko & Padutov 1961). In the captive feeding experiment by Nowakowski et al. (2006), *D. nitedula* significantly preferred animal food over plant food. Animal food (and especially insects) has also been shown as preferable in some other captive feeding experiments (e.g. Angermann 1963, Airapetyants 1983).

That said however, when suitable high-calorie vegetable food is abundant, it may dominate the diet of

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D. nitedula in some parts of the range (e.g. in Central Asia, Caucasus and Moldova) or in particular periods (e.g. in late summer). The composition of vegetable food used by *D. nitedula* is very diverse in different parts of its range. Dormice like both soft sweet fruits such as apricots and high-calorific hard mast such as nuts and acorns (Lozan 1970, Airapetyants 1983, Rossolimo et al. 2001). *D. nitedula* feeding on green parts of plants (buds, young leaves, shoots) has been recorded by several authors in the spring period (Golodushko & Padutov 1961, Holišová 1968, Schedl 1968, Davydov 1984, Lozan et al. 1990). However, according to Airapetyants (1983), dormice did not eat such food in captivity, and green parts of plants were not recorded in dormouse diet in Lithuania.

At the Lithuanian dormouse study site, high-calorific vegetable food is scarce and it is present only for short periods. It should be noted that hazel (*Corylus avellana*) is totally absent at this site, but *D. nitedula* has been recorded feeding on hazel nuts at a second locality in Lithuania. Due to the scarcity of suitable vegetable and animal food in particular periods, dormice are forced to feed on less-calorific or less accessible vegetable food such as female catkins of aspen, seeds of birch and cones of Norway spruce. These vegetable foods as well as more calorific food such as strobiles of Norway spruce, blossoms of oak and fruits of glossy buckthorn have not previously been recorded in the diet of *D. nitedula* elsewhere in the range of the species. Feeding on such foods are peculiarities of the dormouse diet on the north-western edge of its range. The ability of *D. nitedula* to change its diet according to food abundance in the surroundings shows a particularly opportunistic pattern to its feeding and the high adaptability of this species to local conditions.

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