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Review Article

Nutrition of the Edible dormouse (*Glis glis* Linnaeus, 1766) across the distributional range

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Abstract

The edible dormouse is an example of adaptations of mammal nutrition for a long hibernation. Because of the absence of caecum, the food of dormice is rather refined. The animals prefer foods with a significant content of nutrients. The main food is tree seeds, such as beech nuts and acorns. Also, hazelnuts, walnuts, chestnuts, cones, and birch seeds may become the main forages in several localities. All available fruits in biotopes make a significant part of the species' diet. Green parts of plants and animal food are permanent additions. Strong seasonal changes depend on the availability of forages in biotopes present. At the beginning of the active season in May-June tree buds, flowers, leaves, young bark, last-year tree seeds, and invertebrates are the main forages. In July-August, mainly fruits, berries, and unripe tree seeds become the basis of the diet. Before hibernation, high-calorie tree seeds are the most important. Geographical differences determine the species' diet depending on the composition of plant communities in biotopes. Predation of birds is also registered in several regions. In captivity, dormice eat a wide variety of fruits, vegetables, seeds, protein, and carbohydrate forages. Amounts of consumed food considerably exceed daily energy requirements, which provides significant body mass gain during the active period.

Keywords: Beech and Oak Forest, Dormice, diet, invertebrates, seasonal changes

Introduction

The breadth of an animal species' ecological niche is determined mainly by its nutrition characteristics. They influence the variety of adaptations to a particular way of life and the choice of inhabited plant communities (Naqibzadeh, et al. 2022). Even strong restrictions on the life cycle such as hibernation can't reduce the number of general ways of animal nutrition. The edible dormouse is a bright example of the adaptations of an herbivorous species to long hibernation.

Therefore, peculiarities in nutrition must show the most effective ways of fattening and survival during the winter period.

As the edible dormouse is a nocturnal species, direct observations of its nutrition are almost impossible. The most informative invasive methods, such as the analysis of stomachs (Holišová, 1968; Franco, 1990; Lozan et al., 1990; Gigirey & Rey, 1998), are not used currently because of conservational issues. The most popular method is an analysis of feces (Fietz et al., 2005; Sailer & Fietz, 2009; Juškaitis et al., 2015; Vekhnik & Dyuzhaeva, 2022), the disadvantage of which is overestimating the importance of items taken in small amounts (Batzli, 1985). Also, the analysis of residues in hollows (Snigirevskaya, 1953), tests of consumption in captivity (Nowakowski et al., 2006), and radio telemetry studies of the time spent on a particular tree is used (Jurczyszyn, 2018). This variety of methods sometimes doesn't allow adequate comparison of some aspects in different geographic localities but allows to reveal some unexpected peculiarities in several study areas.

According to Formozov (1928), the food of the dormouse is, in comparison with other rodents, rather refined and fancy, the animals prefer forages with a significant content of nutrients, such as nuts, fruits, honey, and insects. These preferences can be inherent only to animals in rich habitats. The diet of most Palearctic rodents is much poorer. This is explained by the characteristic feature of the digestive tract of dormouse, the absence of caecum (Vorontsov, 1967), mentioned by several researchers (Popov, 1960; von Vietinghoff-Riesch, 1960; Rossolimo et al., 2001; Juškaitis et al., 2015; Jurczyszyn, 2018). However, these peculiarities allow the dormouse to exhibit significant seasonal changes in the diet, as well as variability in the composition of food in different parts of the distributional range. In the direction from west to east, changes in the diet are traced, associated with different main fattening forages because of gradual changes in phytocoenotic conditions, mainly a decrease in the role of beech and an increase in the role of oak in biotopes inhabited by the dormouse.

Forages of the species in the different regions

The dormouse is a predominantly herbivorous species. Its main food is tree seeds, such as beech nuts and acorns (Ognev, 1947; Thompson, 1953; Airapetyants, 1983; Kryštufek, 2010). Also, hazelnuts, walnuts, chestnuts, and cones may become the main forages in several localities. Green parts of plants and animal food are permanent additions, which can become important at the beginning of the active season (Donaurov et al., 1938; Holišová, 1968; Gigirey & Rey, 1999; Nowakowski & Godlewska, 2006). Where possible, the species forages on various fruits and berries (von Vietinghoff-Riesch, 1960; Rossolimo et al., 2001). Ognev (1947) indicated a significant difference in the diet of dormice living in the forest, the main food of which is most often acorns and nuts, and those living in orchards, the diet of which includes apples, pears, plums,

etc. These differences were shown also in the studies of other authors (Donaurov et al., 1938; Lozan et al., 1990).

Most authors distinguished two main categories of plant food, including low-calorie and high-calorie forages. Gigirey and Rey (1999), as well as Sailer and Fietz (2009), classified them as fleshy fruits and nuts (this will be used further). Juškaitis et al. (2015) described them as soft mast (berries and other soft fruits) and hard mast (nuts and acorns). Donaurov et al. (1938) distinguished a group of nut-bearing fruits, or oily food, and a group of watery food – fruits and leaves. Grekova (1970) named them nut-bearing and wild fruits. Apart from these main categories, almost all authors reported a permanent admixture of green parts of plants and food of animal origin.

In northwest **Spain** (the Montes do Invernadeiro Nature Reserve) nuts (37% of feces) included acorns and hazelnuts (Gigirey & Rey, 1999). The fleshy fruits detected (46.5%) were mainly blackberry and apple and to lesser amounts bilberry and rowan-berry. Identified leaves (8%) were mostly from *Rubus ulmifolius*; other species were *Quercus robur*, *Betula celtiberica*, and *Ilex aquifolium*. Animal-prey remains (6.9%) were exclusively insects (Hymenoptera, Coleoptera, and Hemiptera), and Arachnida. Fungus remains (1.1%) were mostly ascomycetes of the genus Elaphomyces. The consumption of moss (0.5%) was probably accidental. The studies of seasonal peculiarities of nutrition in autumn were conducted by analysis of both feces and stomachs, which gave rather different data (Gigirey & Rey, 1998; 1999).

In **Belgium** (Belgian Lorraine) nut pulp was the main component of feces (66%). Also, they consisted of plant fibers (49%), and fleshy fruits (27%) with a small proportion of seeds (4%). Nut remains found in nest boxes belonged principally to hazel (*Corylus avellana*), oak (*Quercus* sp.), beech (*Fagus sylvatica*), and hornbeam (*Carpinus betulus*). Remains of arthropods (27%) and bird feathers (11%) were also present (Hürner & Michaux, 2009).

In **Germany** (Deister, Lower Saxony) the main forages were also nuts: acorns, beeches, walnuts, hazelnuts, chestnuts, and other forest seeds (von Vietinghoff-Riesch, 1960). Wild or garden fruits were also in the species' diet, along with berries such as blueberries (*Vaccinium myrtillus*), strawberries (*Fragaria* sp.) (forest and garden), and raspberries. The dormouse likes grapes, from which only seeds are often eaten. In certain periods the dormouse may eat buds, leaves, and needles of trees. Leaves of beech, hornbeam, poplar, and sugar maple (*Acer saccharum*) are consumed, and buds of young shoots, including beech and black elderberry (*Sambucus nigra*). In open enclosures, dormice eat the needles of Weymouth pine (*Pinus strobus*), black pine (*P. nigra*), and larch (*Larix* sp.). The gnawing of young bark is peculiar for the species. The authors observed the eating of the bark of birch (*Betula* sp.), aspen (*Populus* sp.), Canadian poplar (*P.* x *canadensis*), and larch. The composition of animal food included snails and caterpillars, July (*Polyphylla fullo*) and May bugs (*Melolontha* sp.), and common flies (*Musca domestica*).

The study of males' nutrition during the active season in the Botanical Garden at the University of Ulm, **Germany** (Baden-Württemberg) showed that in their nutrition nuts were represented by seeds of oak (*Quercus* sp.) and beech (*F. sylvatica*) and fleshy fruits included raspberries (*R. idaeus*) and blackberries (*R. fruticosus*). Miscellaneous samples contained moss, larvae, and items which were not determinable (Sailer & Fietz, 2009).

In **Slovenia,** the edible dormouse also feeds on beech nuts and acorns (Kryštufek & Flajšman, 2007). Besides, seeds of other trees are in the species' diet, such as hazel, maple, hornbeam, chestnut, spruce, birch, and cypress. Fleshy forages include fruit and berries, for example, dogwood, hawthorn, and blackberry. The species may consume bark, tree buds, flowers, young leaves, and various mushrooms and moss species. Also, the phenomenon of gnawing on limestone in caves is observed.

In **Poland** (Roztocze National Park, southeast Poland) radio-tracking study showed that most of the time dormice was spent on beech (*F. sylvatica*) (91%). Not only nuts but also green parts of the beech were eaten, including buds, leaves, and young bark. Also, the animals foraged on aspen, wild cherry (*Prunus avium*), and hornbeam. Strong differences were found in the nutrition regiment in masting and non-masting years. In non-masting years dormice can spend more time on beech consuming vegetative parts of beech trees. Also, the importance of fruit trees may be very changeable (Jurczyszyn, 2018).

In **Romania,** the diet of dormice is presented by hazelnuts, beech (*F. sylvatica*) seeds, and acorns. Fleshy fruits are collected from blackthorn (*P. spinosa*), wild pear (*Pyrus pyraster*), wild apple (*Malus sylvestris*), cornelian cherry (*Cornus mas*), and blackberry (*Rubus* sp.). Also, buds from trees were consumed, as well as animal food: adults and grubs of beetles, and eggs of small birds (Istrate, 2008).

In **Lithuania,** seasonal changes in the nutritional regiment of the species were studied for several years and differences were found even in the number of forages consumed every year. The main forages there are acorns, hazel nuts, birch seeds, vegetative parts of plants, raspberries, and fruits of glossy buckthorn (*Rhamnus frangula*), fungi, birds, their eggs, and insects. The occurrence of birch seeds and fungi was very changeable, up to absence in certain months and years (Juškaitis et al., 2015).

In **Moldova** and **Ukraine** (the Middle Dnieper region) vegetable forages were found in 58.8% of stomachs and included 14 plant species (Lozan et al., 1990). Nuts in the diet were presented by acorns of pedunculate oak (*Q. robur*) (20%) and seeds of Scots pine (*P. sylvestris*) (20%), hornbeam (14%), hazelnut (12%), walnut (*Juglans regia*) (6%). Fleshy fruits included hawthorn (*Crataegus sp*.) (2%), rose hips (*Rosa* sp.) (2%), strawberries (2%), and blackberries (2%). Other plant forages included knot grass (*Polygonum aviculare*) (2%), sunflower (*Helianthus annus*)

(2%), ladies' purse (*Capsella bursa pastoris*) (4%), cocksfoot panicum (*Echinochloa crus-galli*) (4%), green parts of plants (8%). Impurities of animal food are contained in 41.2% of the feed. Another study in that region added to the list more fruit species: apples, pears, plums, apricots, and cherries (Samarskiy & Samarskiy, 1980). In the territory of Bukovina (Ukraine) in May, in the foothill areas, the remains of dormouse food were found in the form of gnawed acorns, beech nuts, and young spruce cones. In summer and autumn, in the mountainous regions of Bukovina, the main food of the dormouse consisted of spruce seeds (Shnarevich, 1959). In the Transcarpathian region of Ukraine, the dormouse caused strong damage to young coniferous plantations, nibbling the bark on the pre-apex part of spruce and pine (Turyanin, 1959).

In Bryansk Oblast (**Russia**), the main food of dormice is fruits, nuts, acorns, seeds, sometimes insects, chicks of small hollow-nesting birds from the order of passerines (tit (*Parus sp.*), nuthatch (*Sitta europaea*), redstart (*Phoenicurus* sp.), chiffchaff (*Phylloscopus* sp.), robin (*Erithacus rubecula*) (Lavrov, 1983).

In the territory of the Repulic of Tatarstan (**Russia**), stomachs were filled mainly with acorns, blackberries, and, apparently, leaves. In one stomach fragment of the elytra of a small ground, the beetle was found, probably of the genus Amara (Popov, 1960).

In the Zhiguli Mts (Samara Oblast, **Russia**), nuts included acorns of pedunculate oak and hazel nuts (84.6%), and also birch seeds (54.2%) (own data). Fleshy fruit in the diet was replaced by tree leaves (32.7%). Minor food types included mushrooms (48.3%), bark (21.8%), algae and lichens (5.7%), plant seeds (3.8%), and arthropods (45.2%). Bird feathers were found in three samples (0.5%). Plant seeds were represented by blackberry (*Rubus caesius*), thistle (*Cirsium* sp.), knotweed (*Polygonum* sp.), bunias (*Bunias* sp.), bluegrass (*Poa pratensis*), nightshade (*Solanum* sp.), salsify (*Tragopogon* sp.), bluebell (*Campanula* sp.) and water avens (*Geum rivale*). Snigirevskaya (1953), studied the nutrition of leftovers in hollows in the same study area and found that tree leaves belonged to maple (*A. platanoides*), lime (*T. cordata*), pedunculate oak, and spindle-tree (*Euonymus verrucosus*). In the Southern Volga Region, dormice, according to Kozlov (1939, cit. from Ognev 1947), feed almost exclusively on plant foods: acorns, nuts, juicy fruits, and berries.

In the Caucasus (**Russia**), the dormouse willingly eats raspberries, pears, cherries, quince (fruits of *Cydonia oblonga*), and all garden fruits, including walnuts and almonds. In mountainous beech forests, beech nuts and, to a lesser extent, hazelnuts play the main role, and wild fruit trees play a minor role (Geptner, 1932). In the spring, before the fruits and berries ripen, the dormouse feeds mainly on the buds and young shoots of various trees, mainly of the same beech. Also, the dormouse eats the tender bark of young branches of beech, twigs, cherry plum, and other trees, peeling it off with narrow ribbons. According to Satunin (1920), in the Caucasus, the dormouse

also eats acorns, chestnuts, pits of apricots, peaches, as well as the very pulp of juicy, sweet fruits. In Krasnodar Territory, the main food of the species is beech nuts, pears, apples, hazelnuts, and walnuts (Kotov & Ryabov, 1963).

Grekova (1970) studied the feeding habits of animals in different regions of the Caucasus. Among plant food in the zone of hemixerophytic forests (Ciscaucasia, Novorossiysk region) acorns (72.8% of stomachs) were in the first place in feeding. The second most important forage was the green parts of plants (leaves, buds, bark of young shoots) (35.4% of stomachs). The third place in nutrition was placed by seeds of tree species (hornbeam, ash) (23.4%). In this region, the group of animal food was of significant importance for the species (41%). In the foothills of the Caucasus (Maykop region), the most important forage was seeds of wild fruit crops (pears, apples, cherry plums) (49.3%). The second place was occupied by nuts (hazel, partly beech) (33.8%). An essential seasonal food was green parts of plants (34%). The seeds of hornbeam, ash, lime, and maple also had a significant place in the diet of the dormouse (21%). The group of animal food was less important than in the previous region (20.2%). The main food in the mesophytic deciduous forests of the Tuapse region and the Caucasian Reserve was oily seeds of beech, hazel, and walnut (44.4%). The seeds of wild fruit crops ranked second (31.5%). Green parts of plants were in third place in terms of frequency of occurrence. Seeds of oak and other tree species were not used or used in small quantities. The group of animal food was of little importance.

In the Caucasian Reserve, plant food was found in 76.6% of stomachs, and animal food in 23.4% of stomachs (Donaurov et al., 1938). Nuts (42.7 %) were represented by beech (*F. orientalis*) (28.3%) and hazel (7.6%). Walnut fruits were of little importance (2.6%). Watery foods (including fleshy fruits) (31.5%) included pears (*Pyrus communis*) (14.7%), apples (*Malus communis*) (9.1%), cherries (*Prunus avium*), (4.5%) cherry plums (*P. divaricate*) (0.4%), and chlorophyll-bearing parts of plants (6.8%).

The authors also conducted a detailed study of the dormice feeding in the Caucasus, depending on their habitats (Donaurov et al., 1938). On the southern slopes (in the mountains of the Caucasian Reserve), the rodent preferred a group of oily forages (nuts) (54.1%), and of beech nuts (44.7%), walnuts (8.2%), sometimes hazelnuts (1.2%). The dormouse did not eat apples and cherry plum (*P. divaricata*) at all and ate a lot of pears (27.2%) and cherries (12.9%). On the northern slopes in the feeding regiment of the rodent, oily and watery food occupied equal amounts (50.8% and 49.2%). The absence of walnuts was compensated by the large consumption of hazelnuts (17.2%). Cherry and pear fruits were eaten in smaller quantities (0.9% and 13.7%). In the group of watery foods, apples were preferred (21.9%).

There is only general information on the Transcaucasus. In the Vartashen region of **Azerbaijan**, the food of the animals consists of nuts, acorns, and fruits. They also consume animal food,

especially insects (Meyer & Skholl, 1955). In **Armenia**, dormice feed on acorns, beech nuts, seeds, and pulp of various wild and cultivated fruit crops, and eat some insects (Dal', 1954). In **Iran,** the principal diet includes beechnuts, walnuts, and hornbeam seeds (Lay, 1967, cit. from Kryštufek & Vohralík, 2005; Naderi et al., 2014; Ahmadi et al., 2017).

As a whole, the number of nuts species is very low in different regions, which points to their dominant role in the species' nutrition and their essential importance. Both acorns and nuts may be the main forages in optimal and suboptimal habitats. The role of high-energy tree seeds in the life cycle of the edible dormouse is shown by several authors (Bieber, 1998; Milazzo et al., 2003; Schlund et al., 2002; Pilastro et al., 2003; Vekhnik, 2019). Ruf and Arnold (2008) showed that the nutritional composition of food is directly related to the hibernation process.

In contrast, the list of fleshy forage fruit species is wide enough and depends on the current availability of fruits and berries in a certain locality. Their diversity justifies their role only as substitute forages. In the poorer localities, fruits may be absent and their role may be played by green parts of plants.

Thus, the huge distributional range of the edible dormouse, enlarged from British islands on the west to the Volga River on the east, allows for the very high variability of the species' diet. But morphological and biological peculiarities of the dormouse cause high selectivity in nutrition. Analysis of studies showed the dependence of the species' habitation on the distribution of broad-leaved tree species, mainly beech and oak. The current distributional range of the dormouse embraces a large part of the areas of the genus *Fagus* in the Europe-Orient plot distribution (Yim, 1983; Fang & Lechowicz, 2003) and the genus Oak distribution (Eaton et al., 2016), which overlap in a considerable part of areas. But *Glis* distributional range doesn't extend to the north and east as Fagaceae trees probably because of harsh climatic and foraging conditions. In the marginal northern (Lithuania) and eastern (Zhiguli Mts., Russia) populations the dietary spectrum was found the poorest with scarce fruits and such a low-quality type of food as birch seeds, not consumed in other regions. On the contrary, the highest diversity of dietary spectrum among studied plots is observed in the Caucasian region. This is caused by the highest species diversity of trees from the Fagaceae family (Novoseltsev & Bugayev, 1985) and other nut-bearing species as well as various fruit trees in mountainous subtropical areas.

Seasonal changes in the dormouse nutrition

In the diet of the species, seasonality is clearly expressed, associated with the gradual appearance and maturation of its favorite plant objects (Airapetyants, 1983). As most of the descriptions are resented by months, it allows us to compare the data obtained in different localities. The available data are summarized in the table.

Table 1. Seasonal changes in the nutrition of the edible dormouse in different localities.

Country, references	May	June	July	August	September	October
Great Britain (Burgess, 2002)	beech pollen					
Spain (Gigirey & Rey, 1999) (analysis of feces)		fleshy fruit (50%), flowers (>30%), leaves (<20%), arthropods (<5%)	arthropods (>80%), flowers, leaves, and moss (<10%)	fleshy fruit (>90%), miserable proportions of nuts, arthropods, and flowers	fleshy fruit (>50%), nuts (>40%), a small addition of leaves and arthropods (<10%)	acorns and hazel nuts (<70%), fleshy fruit (>20%), leaves (<10%), miserable proportions of arthropods and fungi
Spain (Gigirey & Rey, 1998) (analysis of stomachs)					acorns and hazelnuts (81.2%), blackberry seeds (50%), vegetative plant structures (21.9%), birch seeds (6.2%), moss (37.5%), animal remains (56.2%) in small amounts	
Belgium (Hürner & Michaux, 2009)		plant fibers, arthropods (60%), fleshy fruits (40%), nuts of hazel, oak, beech, and hornbeam (40%), feathers (20%)	plant fibers (84%), fleshy fruit (48%), arthropods (42%), nuts (29%), feathers (26%), a small number of seeds	nuts (>80%), plant fibers (36%), fleshy fruit (25%), small proportions of arthropods, seeds, and feathers	nuts (93%), plant fibres (17%), arthropods (>20%), fleshy fruits (3%)	
Germany (v. Vietinghoff-Riesch, 1960)	birds, buds, young bark, beech cotyledons, leaves, occasionally snails, and insects		walnuts, sweet chestnuts, acorns, beech nuts, leaves, cherries, apples, and plums		nuts, fruits, leaves	
Germany (Sailer & Fietz, 2009)		leaves (63%), arthropods (20%)	leaves (>20%), fruits (51.8%), seeds of beech and oak (3.3%), arthropods (4%)	leaves (<20%) fruits (60.3%), tree seeds (>20%),	tree seeds (81.6%), leaves (6.4%), fruits (13.8%)	
Italy (Kahmann, 1965)		bark, tree buds, flowers, leaves, arthropods, beech nuts, ebony, chestnut, hornbeam, elderberry	beech nuts, acorns, hornbeam seeds, chestnuts	hornbeam seeds, beech nuts, acorns, chestnuts, blackberries		
Italy (Santini, 1978)	male inflorescences of stone pine *Pinus pinea*					
Slovenia (Kryštufek &	flowers, bark,	bark and tree buds, tree seeds, and fruits (hazel, maple, dogwood, hawthorn)			beech seeds, acorns, seeds of other tree species, mushrooms	

Flajšman, 2007).	buds, and young leaves					
Poland (Jurczyszyn, 2018)			mainly seeds of beech and Norway maple, small proportions of seeds of elm, hornbeam, wild cherry, aspen, hazel, pedunculate oak, ash, hawthorn and horse-chestnut, lime, locust, and Norway spruce trees	mainly seeds of beech, oak, fir, and wild cherry, small proportions of seeds of hazel, Norway maple, lime, hornbeam, maple, horse-chestnut, locust, and elm		
Slovakia (Holišová, 1968)		bark and buds of spindle tree (75%), its leaves (2%)		hazel nuts and dogwood (67%), bark and buds (33%), leaves (33%), moss, fungus, and wood tissue in trace quantities		hazelnuts, fruits of dogwood, hawthorn, and common maple (78.5%), leaves, (21.4%) bark (14.3%), and fungi (35.7%).
Lithuania (Juškaitis et al., 2015)	acorns from the previous year, inflorescences of various trees, such as pedunculate oak and Scots pine, Norway spruce and hornbeam, vegetative parts of plants and animal food (birds, eggs, and insects), needles of Norway spruce	inflorescences, soft mast, seeds of birches, needles of Norway spruce, and animal food averaging about 20%	soft mast (raspberries and fruits of glossy buckthorn), birch seeds, acorns, hazel nuts, needles of Norway spruce, animal food	hazel nuts, acorns, wild apples, birch seeds, needles of Norway spruce, animal food	acorns, hornbeam nuts, maple keys, Scots pine cones, birch seeds, needles of Norway spruce, animal food	acorns, hornbeam nuts, maple keys, birch seeds, Scots pine cones, needles of Norway spruce
Moldova and Ukraine (Samarskiy & Samarskiy, 1984; Lozan et al., 1990)	last-year acorns, tree seeds, buds, bark, insects	green parts of plants: flowers, ovaries, fresh herbaceous seeds,	unripe acorns and hazelnuts, hornbeam seeds, juicy fruits, and	acorns, hazelnuts, walnuts, and fruit tree seeds.		

		strawberries, parts of plants of the parsley family (Umbelliferae), unripe acorns, egg shells, insects	berries, including wild cherries, apples, pears, plums, apricots, cherries, strawberries, etc.			
Russia (the Zhuguli Mts) (own data)	birch seeds (50%), leaves (62.5%), mushrooms (87.5%), bark (50%), invertebrates (12.5%), invertebrate prey objects (37.5%), nuts (12.5%), moss (12.5%)	birch seeds (65.3%), nuts (84.2%), leaves (44.5%), mushrooms (48.7%), bark (30.6%), invertebrates (38.5%), invertebrate prey objects (17.4%), seeds (38.5%), moss (6.4%)	birch seeds (70.2%), nuts (74.8%), leaves (32.8%), mushrooms (44.9%), bark (19.7%), invertebrates (24.7%), invertebrate prey objects (10.6%), seeds (24.7%), moss (4%)	birch seeds (10.8%), nuts (98.9%), leaves (11.8%), mushrooms (41.9%), bark (8.6%), invertebrates (26.9%), invertebrate prey objects (16.1%), seeds (26.9%), moss (7.5%)	birch seeds (11.4%), nuts (97.7%), leaves (2.3%), mushrooms (63.6%), bark (2.3%), invertebrates (22.7%), invertebrate prey objects (9.1%), seeds (22.7%), moss (4.5%)	nuts (100%)
Russia (Caucasus) (Donaurov et al., 1938)		cherry (>50%), beech nuts of last year (30%), apple seeds (10%)	Cherry (22.2 %), apple (26-36%), pears (48%), beech nuts of last year (3.7%), cherry-plum (3.7%), green parts of plants (16-22.2 %)	pears (37.5%), apples (12%), beech nuts (31.3-88.9%), hazel nuts, fruits (11.1%).	beech nuts (48.5-49.2%), hazel nuts (20-24.1%), pears (3.4-15.4%), apples (4.6-13.7%), green parts of plants (1.6-10.3%), walnuts (9.2%)	beech nuts (85.8%), walnuts (7.1%), pears (7.1%)
Georgia (Spangenberg, 1935)		insects, mainly May bugs (*Melolontha melolontha*), also *Polyphylum* beetles, the bark of young shoots of willow and cherry plums, mulberry berries, fruits of garden and wild cherry plum	cherry plum, plum, apples, pears, cherries, other garden fruits crops (mainly seeds), seeds of unripe grapes, walnuts and hazelnuts, iron tree fruits	fruits of the iron tree, acorns, beech nuts, medlar, dewberry (*R. fruticosus*)	fruits of the iron tree, acorns, beech nuts, medlar, dewberry	quince, medlar, dewberry, apples, the bark of cherry plum and willow, the fruit of the iron tree, beech nuts

In total, seasonal trends in different localities are quite similar. During the active season, an increase in the calorie content of plant forages is observed. This is naturally connected with the phenological stages of plant vegetation. At the beginning of summer, in May-June, green parts of plants, young bark, tree buds, and flowers are consumed. Also acorns and nuts of the previous year

still remained on the forest floor are eaten. In conjunction with the ripening of various fruits and berries, they appear in the diet of the dormouse. The diversity of consumed fruits depends on their availability in a plant community of a particular region. But during the ripening of tree seeds, their role gradually rises. They are eaten from the beginning of growth and become the main type of food at the end of the active season in all plots studied.

In parallel, a decrease in the consumption of invertebrates occurs, except in Spain and Belgium, where the high proportions of invertebrates were found during the mating season, in July. The authors explain this regularity by the lack of the main forages and needs for reproduction (Franco, 1990; Gigirey & Rey, 1999; Hürner & Michaux, 2009), but in two peripheral populations with low diversity of forages, in Lithuania (Juškaitis et al., 2015) and Samara Oblast of Russia (Vekhnik, 2019), the volume of animal food is not high.

A seasonal event is the gnawing of bark in several regions (Platt & Rowe, 1964; Jackson, 1994). In the Caucasus damage to young shoots of cherry plum and willow was observed after hibernation in spring and before hibernation in October-November (Geptner, 1932; Spangenberg, 1935). Such nutrition may have a therapeutic value before a long hibernation (Spangenberg, 1935). In Gorski Kotar (Croatia) this occurred in the first half of the active season – from late June to early July (Glavaš et al., 2003). Von Vietinghoff-Riesch (1960) gave a review of facts on the gnawing of bark to several authors.

The unsolved question in species nutrition is food stores. Some authors observed this, the others consider it occasional. In Great Britain (Chilterns) it was found that dormice did food stores in hibernation cavities, comprising beech seeds and acorns (Brooks et al., 2012). Popov (1938, cit. from Ognev 1947) found that the stocks in the Caucasian Reserve usually consist of 10-12 beech or hazelnuts, sometimes walnuts and chestnuts. Byome (1925) found up to 30-40 selected nuts and fruit pits collected by the dormouse. Similar data were provided by von Vietinghoff-Riesch (1960). In Germany, the dormouse begins to store food in the nests, usually before hibernation. These nests are not usually used for day stays. Such storages consist of “perishable products”, for example, hazelnuts and fruits. Koenig (1960) observed the creation of such stocks in captivity. However, Airapetyants (1983) argued that the dormouse doesn’t create stocks, and the finds of the remains of acorns, half-gnawed leaves, and beech nuts in nest boxes, are explained that the animals eat part of the food in the shelter. Lozan et al. (1990) wrote the same: the dormouse tries to carry food to a safe place. Then such stocks are used in spring after an emergency. Gigirey and Rey (1999) did not find any evidence of the storage of food. They considered bringing food to nestboxes as predator-avoidance behavior.

Animal food

Analysis of the importance of animal food by the frequency of occurrence doesn't allow formally to establish its role in the well-being of an animal, because a considerable part of animal remains belongs to occasional insects consumed with vegetable food. In all the cited studies all invertebrates are analyzed together, and prey objects have the same meaning as ectoparasites and small sapromycetophages.

For example, in **Spain**, the proportion of arthropods achieved 56.3% of samples in autumn (Gigirey & Rey, 1998). Among them, 66.7% of stomachs with animal remains contained ectoparasites (ticks in 55.6% of stomachs, lice in 11.1% of stomachs). Other arthropods included: unidentified insect remains (44.4%), aphid remains (16.7%), Diptera larvae remains (11.1%), adult *Musca domestica* (5.6%), ant remains (5.6%) and arachnid remains (11.1%). All stomachs contained hairs of dormice.

In **Italy** (Asiago Plateau, Venetian Prealps) the study was conducted in a non-typical biotope (Franco, 1990). The area studied belongs to the Fagetum hydroclimatic area, which is occupied by artificial pure stands of Norway Spruce. Animal food eating increased in absolute values from July to August (more than 40%) and then decreased till October when the percentage of animal matter became slightly greater before hibernation. The proportion of animal food in males' diet was higher than in females' nutrition. The difference in occurrence could achieve 10%. Invertebrates included Lachnidae (27.3% of stomachs, 1-24 individuals); Adelgidae (16.4%, 1-8 adults, 3-7 nymphae); larvae of *Cephalcia arvensis* (12.7%) (Pamphiliidae); one larva of Coleoptera (Coccinellidae) (1.8%), probably ingested during aphid's predation; 1 larva and 1 aphid were not identified.

In captivity, both at the Ecological Station of the Adam Mickiewicz University in Poznań and the Zoological Garden in Poznań (**Poland**), the eating of moths was observed very frequently (Jurczyszyn, 2018). The hunt for moths was also seen under natural conditions in the Roztocze National Park during the observation using night vision devices.

The stomachs of dormice in **Slovakia** contained animal food rather frequently, particularly in June and August, but it was found only as an admixture. Two stomachs contained ants, one contained a flea, and four contained aphids. Others were parts of cuticles (Holišová, 1968).

In **Moldova** and **Ukraine** (Middle Dnieper region), the composition of animal food included the yellow slug (*Limacus flavus*) (5.7%), the gray garden slug (*Deroceras reticulatum*) (8.6%), the amber snail (*Succinea putris*) (2.8%), the ground beetle (*Carabus glabratus*) (8.6%), the summer chafer (*Amphimallon solstitialis*) (2.9%), the May bugs (2.9%), the firefly (*Lampyris*) (2.9%), the pine weevil (*Hylobhis abietis*) (5.7%), the sawyer beetle (*Monochamus galloprovincialis*) (2.85%), the large green grasshopper (*Tettigonia viridissima*) (2.9%), the cricket *Modicogryllus frontalis* (2.85%), the carpenter ant (*Camponotus* sp.) (5.7%), the red ant (*Formica rufa*) (5.7%),

the negro ant (*Formica fusca*) (2.85%), the march fly (*Tipula paludosa*) (5.7%), the blackfly (Simuliidae) (2.85%), the pine-shoot moth (*Rhyacionia buoliana*) (8.6%), the gypsy moth (*Lymantria dispar*) (8.6%), the pear aphid (*Eriosoma lanuginosum*) (5.7%), the garden cross spider (*Araneus diadematus*) (2.85%), the muckworm (2.85%) (Lozan et al., 1990).

In the Caucasian Reserve (**Russia**), according to the studies by Donaurov et al. (1938), the group of animal food is of significant importance for the dormouse (23.4% of gasters). Among animals, the species eat slugs (9.4%), caterpillars (3.8%), millipedes (1.9%), and, finally, beetles (0.4%). The remains of small birds (0.4%) and the wool of a shrew (0.4%) were encountered once. In Transcaucasia (Georgia) Spangenberg (1935) noted for the Lankaran region a massive spring eating of May beetles by the dormouse.

In the Zhiguli Mts (Samara Oblast, Russia) invertebrates were analyzed separately for prey objects and occasional invertebrates (Vekhnik & Dyuzhaeva, 2022). The 510 identified invertebrates, found in 38% of fecal samples, belonged to two types and five classes of invertebrates, represented by 19 orders and 55 families. Among them, the most diverse group were the orders of beetles (13 families) and hemipterans (8 families). Most identified species belonged to the Formicidae family. The range of arthropods serving as dormice prey was relatively narrow and primarily included insects. Specimens represented the families of ground beetles (Carabidae), scarabs (Scarabaeidae), taiga beetles (Sphaeritidae), road beetles (Staphylinidae), leather-winged beetles (Cantharidae), darkling beetles (Tenebrionidae), soldier bugs (Pyrrhocoridae), grasshoppers (Tettigoniidae), braconids (Ichneumonidae and Chalcididae), syrphid flies (Syrphidae), cockroaches (Blattellidae), and spiders of the families Pholcidae and Araneidae. Additionally, slugs (Limacidae) and myriapods (Lithobiomorpha) were found. Ants (Formicidae) could be eaten by dormice not as prey items but as annoying commensals. In general, the results indicated the small role of predation in the feeding regiments of dormice from the Zhiguli Mountains. A higher proportion of invertebrates in the diets of males for both prey objects and other invertebrates was found. The analysis of dormouse diets made it possible to clarify the data on the trophic relationships of the dormouse with invertebrates and to establish ecological characteristics that are not directly related to the search and consumption of food. The variety of incidentally consumed invertebrates included phyllophages, small mushroom eaters, saprophytophages, chortophilous springtails, coprophages, parasites, and eurybiont species (Fig. 1). In general, the analysis of the taxonomy of arthropods in dormice feces made it possible to obtain an imprint of the ecological relationships of the dormouse.

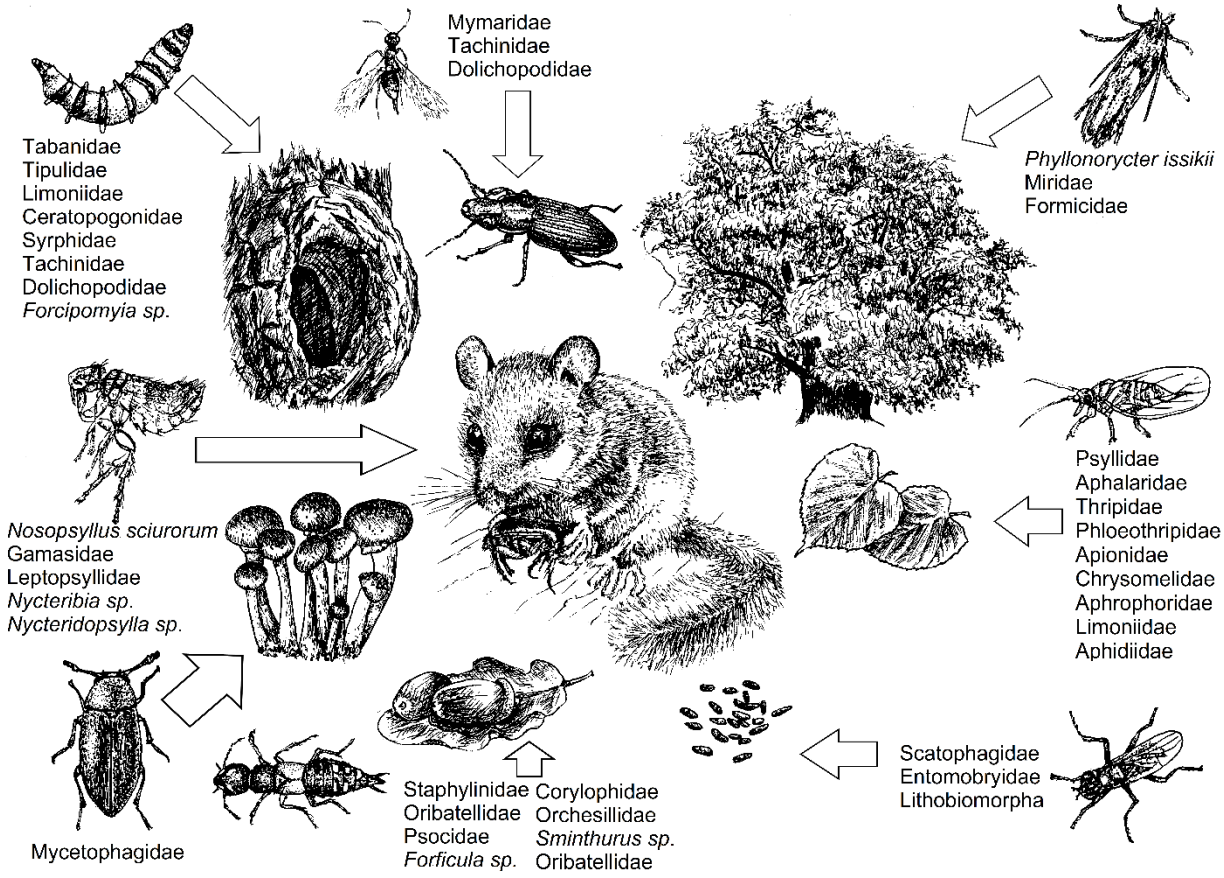

Figure 1. Scheme of the ecological relationships of the edible dormouse, established from the analysis of invertebrates in feces (Vekhnik & Dyuzhaeva, 2022).

Thus, the diversity of prey objects in different regions may have importance mostly at the beginning of the active season. The proportion of invertebrates in all studied regions was highest after arousal from hibernation when high-energetic nuts are still not available. Their role in reproduction was studied by White (2011). But the number of found invertebrate species may be simply the direct function of the number of studied samples (Vekhnik & Dyuzhaeva, 2022).

Predation of the edible dormouse

In several regions, dormice have been reported to prey on birds and their chicks (Lozan et al., 1990; Juškaitis, 2006; Adamík & Kral, 2008; Trout et al., 2012). The role of birds in the diet of the species depended on the method of study and location.

In **Germany** (state of Hessia) special study confirmed the destruction of clutches of eggs, hatchlings, and sometimes adult birds of hole-breeding passerines, mainly great tit (*Parus major*) (46.8%), pied flycatcher (*Ficedula hypoleuca*) (41.6%), blue tit (*P. caeruleus*) (10.4%) and marsh tit (*Poecile palustris*) (1.3%). The predation intensity is increasing because of earlier appearance, caused by climatic changes. The shift for almost 30 years is on average four weeks. Also, a

significant relationship between the population densities of *G. glis* in spring and the number of destroyed clutches of hole-breeding passerines was found (Koppmann-Rumpf et al., 2003).

In the introduced population of **Great Britain**, the rate of damage is also increasing both because of the growth of the number and climatic changes. Authors state that in the last decades the changing climate in Central Europe could create unequal advances in phenology, because of which the edible dormouse advanced its emergence from hibernation faster than woodland birds. The level of nest predation amounted from 25% to 62% of eggs and young for the great tit and the blue tit jointly. The period of predation lasted from the middle of May to the middle of June. Also, cases of predation on the greater spotted woodpecker (*Dendrocopus minor*, *D. major*) were noted (Trout et al., 2012).

In **Germany**, von Viettinghoff-Riesch (1960) presented data on the predation of the dormouse. In Deister (Lower Saxony), the dormouse ravaged nests with eggs and chicks of the pied flycatcher (*Muscicapa hypoleuca*), the Eurasian siskin (*Carduelis spinus*), the bullfinch (*Pyrrhula pyrrhula*), the chaffinch (*Fringilla coelebs*) and others.

In the **Czech Republic** (near Dlouhá Loučka) authors analyzed the data from 1980 to 2005 (Adamík & Král, 2008). They found that the dormouse advanced its phenology by c. 8 days per decade and in the migratory collared flycatcher (*F. albicollis*), the egg-laying dates advanced by 3.5 days per decade; however, non-significant advancement was observed in the resident species: great tit, blue tit, and nuthatch. The timing of breeding in birds had a variable effect between bird species. The number of bird nests destroyed by the edible dormouse during the study period significantly increased in three species: collared flycatcher (from about 5% in 1980-1984 to >40% per 2000-2005), great tit (from <5% to >10%), nuthatch (from about 5% to >10%) and no such change in the blue tit (from about 2% to >5%). The authors acknowledged increasing dormice abundance as the main factor causing high brood losses in birds. During the study period, the occupation rates increased from 2.7% to 19.1%. Later it was found that the majority of cases of nest predation are connected with young males (Adamík, 2014).

In **Lithuania,** the dormouse *G. glis* appeared in nest boxes in the second half of May, when both bird clutches and nestlings were present in nest boxes. The dormouse damaged and ate bird eggs, killed nestlings, and bred adult birds in *Ficedula hypoleuca* (17.4% of nesting cases), *Parus major* (9.6%), *Parus caeruleus* (100%), *Erithacus rubecula* (12.9%). In August, one case of killing European nuthatch *Sitta Europea* in a nestbox was registered (Juškaitis, 2006).

At the same time, no predation was recorded in the forage-rich forests of the Caucasus (in **Russia**). When analyzing large series of stomachs, Donaurov et al. (1938) met only once the remains of a small bird (0.4%) and once the wool of a shrew. Also during the study of feces from live traps in

the Zhiguli Mts., despite low diversity of food items, feathers were found only three times (Vekhnik & Dyuzhaeva, 2022).

Overall, predation has a high significance at the beginning of the active season. Its increasing role in the species' diet may be caused by climatic changes and connected changes in food availability. At the same time, the role of the census method is not excluded: nestboxes fit well for predatory behaviour and their permanent availability may contribute to the more constant feeding on animal food.

Composition and volume of food consumed in captivity

The ratio of the forages consumed in captivity is almost unlimited (von Viettinghoff-Riesch, 1960). In **Germany** (Munden), it contained cherries, apples, pears, plums, peaches, and tomatoes. Blueberries and strawberries were strongly preferred. The diet included also various nuts: beech, acorns, walnuts, hazelnuts, sweet chestnuts, horse chestnuts, peanuts, and wheat seeds. Also, the rodents ate elderberry, gooseberry, and rowan seeds. Bananas and oranges were popular among tropical fruits. Also, dormice consumed cookies, sunflower seeds, dog biscuits, dried fruit, pasta, boiled egg, egg powder, raisins, cake, bacon, and sausage. In early October, oilseeds were preferred over fruits. The requirement for the night for an individual weighing 80 g per day was about 100 g of fresh substance as food and the same was wasted. Regarding the consumption of foliage as a complementary food, in June / July two dormice ate two shoots and seven large poplar leaves in 24 days; in just a month it was 60 leaves. Four dormice ate 500 g of fresh apple substance, of which 100 g were in the form of peel and leftovers, 100 g or slightly more than their weight. There were two apples for each individual per night. On some days, food consumption was even higher but never exceeded 150 g.

In **Austria**, the tamed dormouse ate the following types of food. Wild seeds: acorns (preferable), beech nuts, hazel nuts, walnuts, pine seeds, maple seeds, sweet chestnuts, and horse chestnuts (reluctantly) (von Koenig, 1960). Wild fruits: strawberries, raspberries, blackberries. Buds, foliage, flowers, bark: oak (especially in spring), lime, maple, and other leafy species. Cultivated plants: sunflower seeds (very preferable), hemp, corn, peanuts. Cultivated fruits: cherries, pineapple, strawberries, gooseberries, apricots, peaches, plums, apples, tomatoes, oranges, bananas, grapes, stone and pome fruits, and sometimes seeds. Vegetables: cauliflower, lettuce, carrots (all reluctant). Other products: bakery and confectionery products, jam, honey, sugar, chocolate, and bread. Meat food: brain, intestines, and meat of birds and small mammals, butterflies, grasshoppers, May and June beetles, mealworms, dolls, oak bile, and horse hearts. Liquids: water, sweet and sour milk, and all fruit juices.

In **Italy** (Bagni di Lucca, Tuscany), when studying the daily number of nuts consumed under natural conditions in different years, dormice ate an average of 31.7 and 20.5 nuts per day. In doing

so, they destroyed 84.5% and 91.2% of the walnut crop in the test plot (Rodolfi, 1994). The consumption of nuts was the highest in July.

In **Romania**, the dormouse in captivity consumed vegetable food buds from trees, diverse seeds, hazel and beech nuts, acorns, sunflower seeds, watermelons, ground nuts, *Staphylea* seeds, corn, melissa, rice, blackthorn, wild pears, wild apples, cornelian cherry, blackberry, sweet cherry, wild cherry, apricots, grapes, orange, mild pepper, jam, biscuit, animal food: adults and grubs of beetles, eggs of a small bird and other dormice ex. *Muscardinus avellanarius* (Istrate, 2008).

Nowakowski et al. (2006) performed a study of food preferences including 315 tests in **Poland**. The composition of the tested food consisted of 63 types, including 17 types of animal food and 46 types of plant food. The edible dormouse consumed all kinds of plant food (100%) offered and did not avoid flowers, buds, or bark. Among the categories of plant food distinguished, the edible dormouse did not show any clear preferences. Among arthropods, the edible dormouse ate only moths and crickets.

Lozan et al. (1990) investigated feeding preferences in captivity in **Moldova**. The food included bread, juicy plant foods, potatoes, meat, apples, eggs, cabbage, beets, carrots, tomatoes, biscuits, honey, cucumbers, and other food. First of all, dormouse ate bread soaked in sunflower oil (1.6-9.1% of daily consumption), juicy vegetable feed (melon, watermelon, apricots - 50.1%); apples (about 30%), nuts (5%), eggs (14.4%), meat (12.5%), biscuits (18.6%). They showed particular interest in smelling food: honey, cheese, cucumbers, and strawberries. Water and milk were treated equally. The presence of watery food did not exclude fluid intake.

According to the observations by Geptner (1932) in the Caucasus (**Russia**), the animal is exceptionally voracious, and in this respect, it probably has no equal among rodents. One observer kept three dormice in August, September, and half of October. They ate 272 cherries, 92 pears, 64 apples, 42 apricots, 58 large plums, 25 grapes, 526 gooseberries, 245 seeds of plums, peaches and nuts, and several hundred pumpkins and melon seeds, not counting a fair number of insects. In addition, animals received white bread 24 times.

Donaurov et al. (1938) recorded the food eaten by the dormouse during the day in the Caucasian Reserve (**Russia**) (according to experiments in captivity). The animals ate 51 beech nuts (23.2 g), 21.7 apples (52.9 g), 55.6 pears (33 g), and 29.3 hazelnuts (19.2 g) per day. The authors tried to verify their data with observations in the wild. A pear tree, which was regularly visited by the dormouse, was noted. On average, dormice gnawed up to 54.6 pears per night, which is close to that obtained in captivity. The stomach weight decreased from 2.6 g upon awakening to 1.5 g before hibernation, which is associated with an increase in the amount of concentrated feed in the diet in the second half of the active season.

In the Vartashen region of **Azerbaijan**, dormice were offered white and red mulberries, apricots, cherries, cherry plums, and dogwoods. They did not eat dogwood and red mulberry at all. The dormice willingly ate Orthoptera. The average daily ration consisted of 8-12 g of nuts and 20-30 g of juicy forages (Meyer & Skholl, 1955).

Yiğit et al. (2001) investigated food preferences in captivity in the subspecies *G. glis orientalis*. Dormice were provided by different kinds of food: hazelnuts, chestnuts, walnuts, beech nuts, linden nuts, sunflower seeds, apple, mulberry, strawberry, fig, cherry, grape, acorn, oak leaves, and fresh branches. They readily consumed all forages, except for walnuts. Food consumption was studied by the example of nuts, including the hibernation period. Daily nut consumption varied from 2.0 to 26.1 g during the hibernation period and from 0 to 52 g during the active period. Additional consumption of fruit was about 20 g per day.

Feeding experiments conducted in Poland showed that amounts of the food considerably exceeded their daily energy requirements (Gębczyński et al., 1972). The amount of metabolizable energy consumed daily ranged from 36.7 to 120.6 kcal. Such a large difference in energy intake resulted in different daily body gains, which varied from 0 to 10 g. Overall, the efficiency of the process of growth is very high. The authors even write that such high efficiency has never been observed in other animals.

Laboratory research has established the variability of taste preferences depending on the body condition of animals (Schaefer et al., 1976). The maximum body weight was achieved with the use of lipids. As the dormouse can reach a significant mass due to the carbohydrate intake, some individuals did not use lipids at all.

In the laboratory, the daily ratio of the dormouse was also up to 100 g, and the mass of the contents of the stomach and intestines was up to 23 g (Samarskiy & Samarskiy, 1980). In the special study by Sailer and Fietz (2009), the overall mean quantity of dry food ingested per day was 14.77 g. The difference between the amount of assimilated energy in mating and the pre-hibernation fattening period was revealed, which led the authors to the conclusion that higher energy intake before hibernation was a consequence of higher quantities of food ingested. Body mass increase during the experiment did not seem to be affected by enhanced assimilation capacities. Assimilation rates remained constant.

Thus, the wide nutrition ratio of the edible dormouse in captivity allows for quick switching to new forages in potential new habitats. That is why the species easily adapts to living close to the anthropogenic landscape, e.g., in village neighborhoods, hunting houses, large parks, and hunting cottages (Rossolimo et al., 2001). Currently, the species is increasing its distributional range in Great Britain (Burgess et al., 2003) and on the left-bank area of the Volga in Russia (personal

communication). At the same time, dependence on high-energy forages fastens the increase of the area to mainly broad-leaved forests with energy-rich tree seeds.

Conclusions

The most important role in nutrition and adaptations to the fructification of broad-leaved tree species are obvious for the edible dormouse. In many regions, all parts of trees are used during the activity season, from young bark and tree buds in spring to ripening seeds in autumn. Animal forages serve as such sources of nutrients. The role of both vertebrate and invertebrate objects in the species' diet decreases when the growth of high-calorie plant forages. But the dormouse exhibits significant ecological plasticity, which is manifested in the probability of replacing different groups of forages in the species' diet and significant seasonal change of forages ensuring maximal nutrient intake. The variety of food consumed throughout the range allows the probability of living next to humans and keeping in captivity. Thanks to nutritional adaptation and other features of biology, the edible dormouse occupies new spaces, such as parks and gardens, and even forms independent wild-living populations in new geographic locations.

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