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Review Article

Distribution and habitats of the edible dormouse (*Glis glis* L., 1766)

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Abstract

The distributional range of the edible dormouse mirrors the close relation of its biology with the community of broad-leaved tree species, mainly beech and oak, providing fattening forages and shelters. Biotopes with beech are more peculiar for the western part of the area, in eastern parts various broad-leaved forests with oak species are common, but they considerably overlap. This transition of habitats is obvious in longitudinal directions over Europe and vertical directions in mountainous areas. In a row of places, the species can live in secondary or anthropogenic communities. The main factors of the species distribution are nutrition and the protective properties of biotopes; additional factors are revealed in several local niche-modeling studies. Now the species range consists of three plots, different by climate and plant composition. The largest European plot embracing the territory from Great Britain and Spain on the west to the Vladimir, Ryazan, and Tambov Oblasts of Russia on the east includes mostly broad-leaved and mixed coniferous-broad-leaved forests with beech and oak. The Volga plot includes broad-leaved and mixed forests with oak along the Volga and its inflows and plots of other communities. The third Caucasian-Asian plot includes the territory of Russia, Turkey, Georgia, Armenia, and Iran. This is mainly mountainous areas of the Caucasus, Talysh, and Thrace mountains and adjacent territories, providing habitats with the most various tree composition and many nut-bearing and fruit trees including from the Fagaceae family. Most of the distributional area is fragmented because of anthropogenic activity and phylogenetic history.

Keywords: Edible dormouse, distributional range, Oak and Beech habitats

Introduction

The distributional range of the species reflects both the ecological niche of a species and historical changes in its area. The distribution area of the edible dormouse coincides mostly with the area of the broad-leaved forests of the Old World. This connection, preserved since Eocene, was shown in detail by Formozov (1928) as early as in the first half of the last century. At that if for the western parts of the area “the geographic range of beech trees (*Fagus sylvatica* and *F. orientalis*)

approximatively coincides with the range of the edible dormouse" (Carpaneto & Cristaldi, 1994), then for eastern parts (Russian Plain) the researcher mirrors "almost complete coincidence of the area, occupied by dormice, with the area of distribution of the oak (*Quercus pedunculta*)" (Formozov, 1928; translated from Russian). Therefore, the distribution area of the dormouse is the gradient from beech to oak forests, excluding some marginal areas and plots of secondary communities. Modern genetic studies confirm the dependence of contemporary areas on the historical distribution of broad-leaved forests with representatives of the Fagaceae family of trees (Michaux et al., 2019; Naderi et al., 2014). But this dependence is not complete, especially in northern boundaries and Asian parts of the distributional range as well as in the vertical distribution of the species. Distributional ranges of beech and oak species are much larger than the current area of the edible dormouse (Fang & Lechowicz, 2006; Eaton et al., 2016).

There are two main factors, determining the species distribution. The main food sources of the dormouse throughout the species range are beechnuts, acorns, hazelnuts, as well as fruits and berries. The diet of dormice also includes small amounts of invertebrates. In spring green parts of trees are also consumed (Ognev, 1947; von Vietinghoff-Riesch, 1960; Airapetyants, 1983; Kryštufek, 2010; Vekhnik & Dyuzhaeva, 2022). The main fattening forage for the dormouse is tree seeds. Their number determines the survival rate of the species during the hibernation period (Fietz et al., 2005). The life cycle of the edible dormouse is closely related to the frequency of tree masting (Schlund et al., 2002; Ruf et al., 2006; Pilastro et al., 2003; Bieber & Ruf, 2009, Vekhnik, 2022).

The next most important factor of habitation is the abundance of places for building nests and breeding offspring. In this connection, the dense undergrowth plays the main role. Dormice are very picky in choosing shelters for daytime rest, and even more so for breeding juveniles (Danilovich, 1938). Shelters should be sufficiently hidden, inaccessible, dark, reliably protected from rain, and have, as a rule, two entrances and are usually located at a height of 4–5 m (von Koenig, 1960; Ayrapetyants, 1983). Hollows are the most frequent shelters of the dormouse (Grekova, 1966; Ognev, 1947; Istrate, 2008b; Krannich et al., 2017). The rodent builds nests in the hollows of oaks, beeches, hornbeams (*Carpinus betulus*), aspens (*Populus* sp.), wild apples (*Malus* sp.), pears (*Pyrus* sp.), iron tree (*Parrotia persica*), and other trees (Ognev, 1947; Meyer & Scholl, 1953; Ayrapetyants, 1983). In a special study in Poland, the most preferred tree species for daily roosts were silver birches (*Betula pendula*) and sessile oaks (*Q. petraea*) (Iwińska et al., 2020). A very common shelter for dormice is caves (Ayrapetyants, 1983; Polak, 1997; Vekhnik & Panteleyev, 1996; Vikyrchak & Ploshchanskiy, 2020). The dormouse also may live in earthen holes between the roots of large trees, for example, beeches (Ognev, 1947; Dal', 1954; Kadatskiy, 1964). Sometimes its habits in the bird nests (Danilovich, 1938; Ognev, 1947). Dormice also settle in attics of houses, hives, and behind wall coverings (Geptner, 1932; Spangenberg, 1935; von Koenig, 1960;

Morris, 2004). They often find shelter in the hunters' cabins or cottages built near the forests (Lozan et al., 1990; Istrate, 2008a). Dwelling in bird nest boxes is very common for dormice (Grekova, 1966; Adamík & Král, 2008), which is a reason for using of special nest boxes for dormice in scientific research (Kryštufek et al., 2003; Morris & Morris, 2010; Bieber & Ruf, 2009; Vekhnik & Vekhnik, 2018).

A comprehensive survey of the habitats of the dormouse seems to be a rather difficult task since modern studies cover only a small fraction of the species range. Thus, the presented review is largely not a collection of the most suitable habitats of the species, but an overview of the phytocoenological characteristics of the places where dormouse studies were conducted, described with varying degrees of detail. It is possible that in some cases the habitats are not optimal, but they confirm the possibility of living in a particular biotope. In many cases, data on habitation in specific places were obtained by specialists over the past century.

Distribution

The distributional range of the edible dormouse occupies most of Europe, the Caucasus, and Asia Minor (Airapetyants, 1983). The structure of the range is represented by three geographically delineated plots, first identified by Likhachyov (1972) for the Soviet Union. The western populations belong to the most extensive European plot, the eastern ones to the Volga plot, and further to the south the Caucasian-Asian plot is located. Between the European and the Volga plots, there are separate finds of the dormouse, and the Caucasian plot is completely separated from the Volga plot by large steppe spaces.

The western border of the range passes through the introduced population of Great Britain, France, and Spain. The eastern border runs mainly along the right bank and at one point the left bank of the Volga river in Russia, the northern one goes from Great Britain through northern France, southern Belgium, northern Germany, Poland, Latvia, and Lithuania, then in Russia through Smolensk, Moscow, and Nizhniy Novgorod oblasts to the Volga in the Republic of Tatarstan. The southern areas of distribution cover the Mediterranean countries, Turkey, Azerbaijan, and Iran. Detailed reviews of the finds of the dormouse, mainly of the first half of the 20th century, are given in the monographs of Ognev (1947) and von Vietinghoff-Riesch (1960). The modern distribution here is shown from the west to the east (Fig. 1).

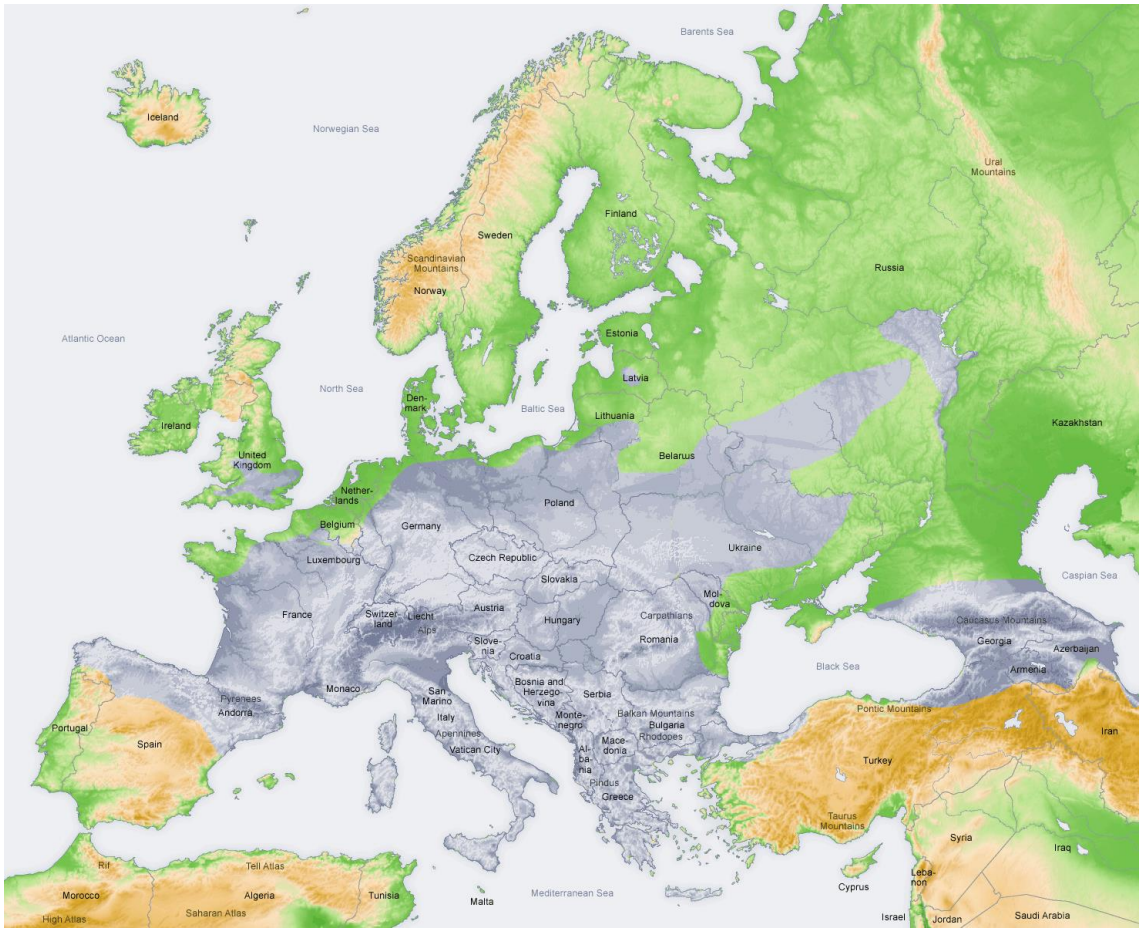

Figure 1. Distribution of the edible dormouse (*Glis glis* L., 1766)

European plot of the distributional range. In **Great Britain**, the dormouse was introduced in 1902 by Lord Rothschild (Thompson, 1953). Now it dwells mainly in central England (Chiltern Hills) (Burgess et al., 2003). Current records are given in NBN Atlas (https://records.nbnatlas.org). On the Iberian Peninsula (**Spain**) the most southern population in Europe exist (Montseny & Montnegre) (Ballesteros et al., 2017).

In **France,** the species is generally widespread in most of France except the Atlantic coastal regions and Brittany (https://inpn.mnhn.fr/espece/cd_nom/61648?lg=en).

In **Belgium**, the edible dormouse area is restricted to a limited area in the extreme south of the country in Wallonia (Schockert et al., 2017).

In **Luxemburg,** the dormouse concentrates mostly in the Minette region and the Mullerthal area (Schlichter, 2011).

To the south, the dormouse lives in **Switzerland** (Eiberle, 1977).

Further, the species lives in **Greece** and its islands (Dimaki, 1999; Grano & Cattaneo, 2012).

In **Poland**, the distribution of *Glis glis* is uneven. The occurrence of UTM-squares is given by Jurczyszyn (1997). In the northern and central parts of the country, several isolated areas are present, and much more sites of different sizes have been preserved in the east and south of the country.

In **the Czech Republic**, according to the survey by Anděra (1986) of former Czechoslovakia, dormice are missing in lowland afforested areas. The species is the most common in the Děčínská vrchovina Highland, the Krušné hory Mts., and the České Středohoří Mts. Highlands in the lower parts of the Berounka and Sázava rivers form the second center of the more frequent occurrence of *G. glis* in Bohemia. From this region, the area of distribution reaches up to Prague in the north and the Plaská vrchovina Highland in the west. The occurrence in the remaining area of Bohemia is sporadic. In Moravia, the occurrence of dormice comprises the Eastern Sudeten and presumably a great part of highlands and uplands belonging to the Českomoravská vrchovina Highland and the Western Carpathians System. The distribution model by standardized mapping grid of the dormouse in the Czech Republic is given in the work by Adamík et al. (2019). Some recent finds are known from West Carpathians (Mikes, 2013). Most of them lie in the Czech Republic and only one is from Slovakia. The elevation range of localities is 290-950 m a.s.l. In most cases, edible dormice were observed in cottages, cabins, or chalets located on the edge of woodlands.

In **Slovakia**, the occurrence of *G. glis* is also concentrated primarily in the uplands, highlands, and mountains of the Western Carpathians System (Anděra, 1986).

In **Hungary** map of *Glis* distribution by UTM-squares is presented by Hecker et al. (2003), which shows the concentration of the species in northern and western parts of the country, including the vicinities of the Danube River (Hecker & Bakó, 2008).

To the south, the species lives in **Slovenia** (Kryštufek & Flajšman, 2007).

The natural southern boundary exists in the Balkans. The species-area in **Croatia** includes Adriatic islands (such as Cres, Krk, Hvar, Bračc, Korčula, and Mljet) and two east Adriatic peninsulas (Kršete, Istria, and Pelješac). Also, the samples confirmed habitation in **Serbia** and **Macedonia** (Konjević et al., 2003; Koren et al., 2015).

To the east, the dormouse lives in **Romania** (Transylvanian Plateau) (Istrate, Bivoleanu et al., 2022) and Bulgaria (Markov, 2012; Nedyalkov et al., 2022).

In **Latvia**, the most northern populations of the species live in the valleys of two rivers – the Gauja and the Daugava in central Latvia (Pilāts et al., 2009). The distribution of the dormice there was mapped using a standard European UTM-grid system. The Gauja River is currently the northern border of the range of the edible dormouse (Pilāts, 2003).

In **Lithuania** localities of *G. glis* are concentrated in the southern part of the country along the two biggest rivers – the Nemunas and the Neris. Dormice are extinct in two localities where they were recorded in 1936, and presumably in some other sites (Juškaitis & Augutė, 2015).

In the south of **Belarus**, the dormouse lives in Brest (Belovezhskaya Pushcha), Gomel (upper reaches of the Berezina River), and Mogilev Oblasts (Likhachyov, 1972; Krapivko, 1999; Gaiduchenko, 2013).

The rodent is widespread in many regions of **Ukraine**, located in the territory of the Polesye Lowland, forest-steppe, and the Carpathians (Kryzhanovskiy & Emelyanov, 1988). The species was found in Kyiv and Kharkiv Oblasts. Also, it lives in Transcarpathia (Transcarpathian, Chernivtsi oblasts). North of the Carpathians, the finds were noted in Lviv, Ivano-Frankivsk oblasts, north of Ternopil Oblast, in the south of Khmelnytsk Oblast, Volyn, Rivne, and Zhytomyr Oblasts. In the floodplain forests of the Dnieper, the dormouse was found in the Cherkassk, Kirovograd, Poltava, and Dnepr oblasts (Shnarevich, 1959; Bezrodnyy, 1991).

In **Moldova**, the species inhabits mainly the Kodry Reserve. Occasionally occurs in the floodplain forests of Transdniestria (Lozan et al., 1990).

To the northeast, dormice live in Bryansk (Lavrov, 1983; Sitnikova, 2016) and Kaluga (Koryavchenkov, 2017) oblasts of the European part of **Russia**.

To the east of the European plot, there are vast forest areas, where only separate finds of the dormouse were noted, mainly in floodplain areas. Single observations were registered in Oryol (Danilovich, 1938, 1941), Smolensk (Likhachyov, 1972), Moscow (Ognev, 1947; Emelyanova, 2008), and Vladimir oblasts (unpublished data). In the north of Tula Oblast, there were several finds along the Oka River (Ognev, 1947; Myasnikov, 1976; Shvets, 2013).

The edible dormouse was found in the territory of Ryazan Oblast in the floodplain forests of the river Pra, in the territory of the Oka Nature Reserve, in the lower reaches of the Moksha and the Tsna rivers and other points (Borodina, 1960; Shaposhnikov, 1971; Onufrenya, 2011). The point of capture of the dormouse in the Tambov Oblast is somewhat isolated. The animal was found there in 1963 in the floodplain forests of the river Tsna (Likhachyov, 1972).

The **Volga plot** of the distributional range is a strip of mainly floodplain oak forests on the right banks of the Oka and the Volga rivers and their inflows (Likhachyov, 1972).

In Nizhniy Novgorod Oblast, the dormouse was noted by several researchers, including in the valley of the river Seryozha (Formozov, 1926; Kaplanov & Raevskiy, 1928; Puzanov, 1955). There are recent local finds in the region (Dmitriyev et al., 2014; Krivonogov et al., 2019).

The species was recorded in the Republic of Mari El on the right bank of the Volga (Baldayev & Korneev, 2015). In the Republic of Tatarstan, the dormouse is relatively common in the riverside oak forests of the Volga right bank, to the south of the confluence of the Sviyaga (Popov, 1960; Galanin et al., 2017). In the Chuvash Republic, the edible dormouse was caught in the forests along the watershed of the Sura and the Tsivil rivers, including the territory of the Prisurskiy Nature Reserve (Puzanov, 1955; Popov, 1960; Glushenkov, 2018). Currently, *G. glis* inhabits coniferous and broadleaved forests of the Republic of Mordovia (Astradamov & Tugushev, 2005; Andreychev, 2020).

Only a few finds are known in Penza Oblast (Ilyin et al., 2006). In Ulyanovsk Oblast, the dormouse was found in several areas along the right bank of the Volga (Titov, 2015).

To the south and east along the Volga, the dormouse was found in the Zhiguli Mountains (Popov, 1960; Vekhnik, 2020). On the left bank of the Volga, the dormouse lives in the Sokolyi Mountains and parks of Samara city where it reaches the eastern limit of distribution (Rigina, 2004, own data). Lower along the Volga the species lives in Saratov and Volgograd oblasts (Ognev, 1947; Kubantzev, 1962; Belyachenko, 2021).

Further, the **Caucasian-Asian plot** of the species distribution is located. The Caucasian plot includes Europe and Asia territories. The dormouse is widespread throughout the Caucasian Territory, starting in the northwest of Novorossiysk (Ognev, 1947). The upper limit of distribution is 2000 m (Zharkov, 1971).

In the Ciscaucasia, the dormouse is widespread in the Stavropol Territory (Likhachyov, 1972) and the Krasnodar Territory (Meyer & Scholl, 1955; Grekova, 1966; Kharchenko & Minoranskiy, 1967). Transcaucasian distribution of the dormouse embraces most of the forested areas except for the Kars Upland, including Northern and South Ossetia, Dagestan, and Chechnya (Satunin, 1920; Ognev, 1947).

Shidlovskiy (1954) gave an overview of the finds of the dormouse in **Georgia** in the middle of the last century. The species was widespread throughout the zones of the Main Caucasian Ridge and the Lesser Caucasus. Then four individuals of dormice were captured in the eastern mountain-forest belt of Adjara (Alania et al., 1971).

In recent surveys, dormice have been found in all 7 surveyed regions of **Armenia**. Dormice are most often found in the northern forest regions: Tavush, Lori, and partly Kotay regions (Dal', 1954; Sahakyan, 1964; Sargsyan & Yavruyanya, 2019).

The species lives in **Azerbaijan**, including in the forest belt of the Zakatala state reserve (Vereshchagin, 1959; Popkova & Popkov, 1965).

To the south and the west of the Caucasus, the dormouse lives along the Black Sea, Marmara, Thrace, and other regions of **Turkey** (Helvaci et al., 2012; Selçuk et al., 2012). In **Iran,** the species distribution is limited to the Hyrcanian Forests (Naderi et al. 2014, Ahmadi et al., 2018).

Biotopes

According to microstatic conditions, the places inhabited by this species are characterized by a low percentage of humidity, average illumination, and the presence of rotten stumps, trunks, old hollow trees, and dense crowns (Lozan et al., 1990). Favorable factors for the habitat of the species are the variety of deciduous species, the presence of wild fruit trees, and berry bushes. The dormouse willingly inhabits hilly areas accessible to the sun, overgrown with mixed or deciduous forest

(Ognev, 1947). The height of distribution of the species in mountainous areas is usually about 1000 m (von Vietinghoff-Riesch, 1960).

According to the in-depth study conducted in Spain, the distribution area of *Glis* is characterized mainly by presenting milder summer temperatures and more stable rainfall throughout the year and more predictable from one year to another, concerning the rest of the unoccupied territories, or where the July mean temperature values exceeds 23ºC or less than 40 days with rainfall are recorded (Castro & Real, 2007).

Biotopes in European Plot. Most of the described biotopes in Western Europe are characterized by the presence of beech in the composition of the stand, however, different oak species are quite common. In the introduced population of Great Britain, on the western border of the range, the species lives in deciduous woodland, mainly stands of European beech (*F. sylvatica*), with an admixture of spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Hockeridge Wood, near Berkhamsted, Hertfordshire) (Morris & Morris, 2010; Brooks et al., 2012).

In Germany the studies of the dormouse were conducted in the biotopes, the proportion of oak and beech in the composition of the stand of which was significantly different, creating different conditions for the population and the formation of life cycles. Long-term studies have been conducted in southwestern Germany in the state of Baden-Württemberg near Tübingen (Fietz et al., 2014). In one cite the European beech was the dominating tree species in both study areas, but oaks, hornbeams, pines, and spruce also occurred (Schlund & Scharfe, 1997). Another study was conducted in two plots: deciduous forest and coniferous–mixed forest located 1 km apart. At the first site, approximately 50–70% of all trees were up to 150-year-old beech and up to about 20% of oak trees (*Q. robur, Q. petraea*), while another one was dominated by 100-year-old pine with 20% spruce and 20% beech trees (Schlund et al., 2002). Also, dormice were studied here on a small mountain, the Spitzberg, in a Scots pine-dominated forest with oak and European beech (Randler & Kalb, 2020).

In central Germany, one of the studies were conducted in the vicinities of Frankfurt am Main, Germany. The habitat of the edible dormouse here was the mixed forest consisting mainly of oak (*Q. robur, Q. petraea*), European beech, and hornbeam (Scherbaum-Heberer et al., 2008). Another study in that region (near the town of Steinau an der Strasse) was carried out in mixed deciduous woodland of approx. 120 years old with pedunculate oak, European beech, and hornbeam and developed shrub layer (Koppmann- Rumpf et al., 2012).

Near Marburg study of dormice was conducted in three different sites. One of them was the edge of a deciduous beech forest with the understorey at the forest edge including elder (*Sambucus nigra*/*S. racemosa*) and blackthorn (*Prunus spinosa*). Some trees of other species occurred, such as pedunculate oak, spruce, European larch (*Larix deciduas*), willow (*Salix* sp.), and hornbeam. The

second trapping site consisted of bushes, mainly rose (*Rosa canina*), blackthorn, hawthorn (*Crataegus monogyna*/*C. oxyacantha*), elder, raspberry (*Rubus idaeus*), blackberry (*R. fruticosus* agg.), hazel (*Corylus avellana*), hornbeam, and some isolated trees (ca. 14–20 m height; beech, sessile oak, pedunculate oak, common walnut (*Juglans regia*), small-leaved lime (*Tilia cordata*), sycamore maple (*Acer pseudoplatanus*), locust tree (*Robinia pseudoacacia*), willow, Scots pine, and spruce). The third site was similar, but large seed trees were not present. All sites contained several fruit trees like wild apple, pear (*Pyrus communis*), sweet cherry (*Prunus avium*), and plum (*Prunus domestica*) (Bieber & Ruf, 2009). In the vicinity of Zurich (Switzerland) (Eiberle, 1977), the species prefers mixed forests with beech, ash, oak, and hornbeam. The dormouse avoids pure conifers and plantations of single deciduous species. In Austria, the maximum distribution of the dormouse falls on the area of distribution of beech forests along the northern and western edges of the Alps, as well as in the southeastern marginal Alps. Finds of dormice in the alpine region refer to the heights between 150 m and about 1600 m, most often in the foothill-low-mountain areas between 250 and 700 m (Wettstein, 1963; Kofler, 1969; cit. from Rossolimo et al., 2001).

In Lower Austria, the study of dormice was conducted near Vienna, in the Vienna Woods, Austria, altitude of 400–600 m a.s.l. The plot included deciduous forests dominated by European beech (60%) and spruce (15%), and rarely with pedunculate oak (<1 %) (Hoelzl et al., 2015).

In northern Italy, in the southern part of the Alps, in Cansiglio Regional Forest, dormice were studied in the large woodland, located at an altitude of 1000 m, dominated by European beech, mixed with spruce, fir, and sycamore maple (Pilastro et al., 1996, 2003). In Slovenia, dormice live in old broad-leaved forests with beech and avoid pure beech plantations. The height of their distribution reaches 1200-1300 m. (Kryštufek & Flajšman, 2007). A nest box study was conducted on Mt. Kočevski Rog (south-central Slovenia). Two study sites were mainly in mixed European beech and fir forest (Kryštufek et al., 2003).

The territory of Poland provides a wide variety of biotopes from marginal in the north to the optimal with beech dominating in the south. In western Poland (Sieraków Landscape Park) dormice live in the forest with a share of beech of nearly 30% (Jurczyszyn, 2018). Less numerous species are Norway maple (12.2%), hornbeam (11.6%), elder (7.7%), hazel (6.7%), alder (*Alnus* sp.) (6.5%), ash (6%), pedunculate oak (5.5%), locust (5.3%), sycamore maple (3.9%), small-leaved lime (1.2%), Scots pine (1.1%) and dogwood (*Cornus* sp.) (1%). The remaining species: elm (*Ulmus laevis*), horse chestnut (*Aesculus hippocastanum*), aspen (*P. tremula*), hawthorn (*Crataegus monogynies*), wild apple, silver birch, spindle (*Euonymus europaeus*), spruce, common pear (*Pyrus communis*), European yew (*Taxus baccata*) and currant (*Ribes* sp.) form less than 1%. In Southern Poland (the Pieniny National Park) the most preferred habitat is the forest with beech predomination, also dormice occur in fir and spruce-dominated forests (Jurczyszyn et al., 2018).

In southeast Poland (Roztocze National Park) dormice were found in the biotopes where the dominant tree species were European beech (81.9%). Other species were elder (4.9%), aspen (4.4 %), silver fir (*Abies alba*) (4.3 %), rowan *Sorbus aucuparia* (1.4 %), and wild cherry (1.2 %). Minor species such as Scots pine, spruce, hornbeam, oak, common pear, guelder-rose (*Viburnum opulus*), and silver birch were less frequent (< 1% each) (Jurczyszyn, 2018). In the Carpathians (Ukraine), dormice live in beech forests (middle belt of mountains at an altitude of 600-1200 m) (Lozan et al., 1990).

Many other study areas included both beech and oak as well as other tree species. One of the studies was conducted in southern Slovakia (environs of the village Slávec) in the forest massive including hornbeam, sessile oak, large-leaved lime (*T. platiphylla*), hazel, hawthorn, rowan, mountain ash (*S. aria*) and dogwood. Also, there were scattered walnuts, European beeches, ashes, common maples (*A. campestre*), barberries (*Berberis vulgaris*), the mahaleb cherry (*P. mahaleb*), and spindle trees (*Euonymus verrucosa*) (Holišová, 1968). To the south, according to the distribution study in Hungary by UTM-squares, dormice are most frequent in areas dominated by sessile oak. Dormice are less common in the closed beech stands with sparse understorey. Also, dormice were found in robur-dominated forests and introduced forests, predominantly in black locusts (Hecker et al., 2003). One of the studies (Naszály-hill, near the city of Vác in the northeastern part of the Danube Bend) was conducted in a forest dominated by sessile oak with dense undergrowth (Hecker & Bakó, 2008).

A special study in central Italy investigated the connection between the type of forest management and the distribution of the species (northern Latium, province of Viterbo). Dormice live there mainly in the forest with the predomination of oaks and beech. A close association between the presence of dormice and high forests with low stem number, and, to a smaller extent, rotational forests, was found. Also, the probability of finding was associated with woodlots of 40–50 ha area and more (Capizzi et al., 2003). Despite the wide distribution of beech in the Western plot, described habitats with predomination of different oak species are numerous here. In the westernmost part of the natural distributional range, the researchers consider such habitat optimal for dormice (Gigirey & Rey, 1998). The study was carried out in the Montes do Invernadeiro Nature Reserve in northwest Spain. This area (altitude 1000-1300 m a.s.l.) was largely occupied by montane deciduous woodland. The dominant tree species were pedunculate oak *Q. robur*, other common species were sycamore maple, hazel (*Corylus avellana*), ash (*Fraxinus excelsior*), Iberian birch (*B. celtiberica*), and rowan (*Sorbus aucuparia*). The understorey was dominated by holly (*Ilex aquifolium*) and brambles (*Rubus* sp.).

One of the studies in Central Germany (Thuringia, Altenburger Land) was conducted in pedunculate oak and hornbeam-dominated forest with small-leaved lime, maple (*A. platanoides*, *A.*

pseudoplatanus), and ash. The understorey included elder, hazel, European bird-cherry (*Padus avium*), hawthorn, and blackberry (Worschech, 2012).

In north-eastern Poland (the Bialowieza Forest) the study was conducted in the oak-lime-hornbeam forest (*Tilio carpinetum*) with hornbeam, oak, Norway maple, silver birch, and spruce as the dominant canopy species (Ściński & Borowski, 2008). Hazel and hornbeam formed the understorey. Part of the area was covered with a swamp alder-ash forest (Fraxino-Alnetum).

In the interior part of Croatia, the dormouse is distributed up to the subalpine area (altitude of 1670 m above sea level). The species is quite closely attached to oak groves on mountain slopes with karst microrelief or rocky outcrops (Rossolimo et al., 2001).

On the northern boundary of the range, in Latvia, *G. glis* shows a clear preference for areas with old-growth oaks having wide canopies (Pilāts et al., 2009). Mainly forest edges with more dense understorey and old oaks are the most preferable biotopes. Nestbox study was realized in two sites of Gauja National Park. One of them was situated on the southern slope of the Gauja valley, covered mainly by 60 to the 140-year-old, mixed broad-leaved forest with oak, small-leaved lime, birch, aspen, pine, spruce, and shadbush (*Amelanchier* sp.). Another one was covered mainly by mixed 80 to the 100-year-old forest with lime, birch, and aspen dominating and oak, pine, and spruce as minor species.

In Lithuania, the dormouse prefers mature mixed forest stands with old pedunculate oak trees (Juškaitis, 2006). Old oak trees and old hazels grow in nine out of ten localities of *G. glis*. Nestbox studies were conducted in three plots. One of them was situated in the Kaišiadorys district. The site was dominated by mature (about 150-year-old) tree stands, mainly of oak, Scotch pine, and spruce. Another plot in the Vilnius district was established in the valley of the rivulet Dūkšta. The valley was overgrown with deciduous trees, mainly oaks. Studies of dormouse biology were carried out also in the Rumšiškės forest. The study site was covered by the mixed forest stands composed of 180-year-old Scots pine, 185-year-old pedunculate oak, and 135-year-old spruce with small-leaved lime, birches (*B. pendula*, *B. pubescens*), hornbeam, and aspen. Hazel, rowan, honeysuckle (*Lonicera xylosteum*), and glossy buckthorn (*Frangula alnus*) formed the understorey (Juškaitis & Augutė, 2015; Juškaitis et al., 2015). The special study of biotope preferences showed that dormice prefer nest boxes in mature mixed forests with coniferous trees in the canopy. Important factors were the total cover of oak trees and the number of logs lying on the ground, as well as the total number of dead trees and trunks, providing shelter (Juškaitis & Šiožinytė, 2008). In central Romania (Transylvanian Plateau) the forests inhabited by the dormouse belong to the following main species: the Dacian Tatar maple oak-hornbeam forest and the Dacian oak-hornbeam forest (Istrate, 2008b).

In Moldova, oak, oak-hornbeam and maple-lime-oak forests are optimal for the dwelling of dormice (Lozan et al., 1990). The upper layer is formed by the pedunculate oak with the admixture of ash,

in the second layer hornbeam occurs with the admixture of maple, sometimes sycamore maple, small-leaved lime, and elm. The undergrowth consists of hazel, European spindle tree, honeysuckle, dogwood, and hawthorn. Maple-lime-oak forests are similar but in the second tree layer, Norway maple and small-leaved lime are present. A bit less suitable biotopes are mixed forests with poorer rich tree composition. The higher tree layer is pine, lower one includes pedunculate oak, hornbeam, Norway maple, small-leaved lime, aspen, alder, less often silver birch. In the undergrowth hazel, European spindle, red elderberry (*S. racemosa*), rowan, and rose are present. The least preferable forests are floodplain deciduous and partly ravine forests, as well as the southern steppe forests. The presence in the forest of wild pears, apple trees, and gardens adjacent to the forest is of great importance.

In the Middle Dnieper Region of Ukraine, the dormouse sporadically occurs almost in all forests (Belik et al., 1984; Lozan et al., 1990). Here the species lives in deciduous-coniferous forests, to a lesser extent deciduous ones. The highest and most stable population of the dormouse in this territory is in oak-pine and oak-hornbeam-pine forests with a predominance of Scots pine, pedunculate oak, ash, small-leaved lime, and black alder. Further to the south, in the forest-steppe of Ukraine, the main habitat of the dormouse is also broad-leaved forests, especially old and middle-aged with a predominance of oak and hornbeam, hornbeam with a well-developed undergrowth of hazel, hawthorn, honeysuckle, as well as areas with a significant number of wild fruit trees. The species is also common in mixed forests with a predominance of deciduous species (oak, maple, lime, birch, etc.) and an insignificant admixture of Scots pine. Outside the forest, it also occurs in orchards, forest belts, and vineyards (Samarskiy & Samarskiy, 1980). In Chernihiv Oblast Danilovich (1938) found dormice in places where deciduous forests predominated, including mainly oak, aspen, maple, and some other species. The admixture of coniferous plantations in these forests was relatively small, the spruce here has the southern limit of its distribution and may occur as separate trees.

In mountainous territories, the natural transition from habitats with beech to biotopes with oak domination can be traced. A wide study of habitat preferences was undertaken in northern Sicily, the Madonie mountain range, within a Natural Regional Park (Marteau & Sarà, 2015). At higher altitudes (2000-1300 m a.s.l.), the massif is characterized by beech forests (Anthrisco-Fagetum aceretosum) of the Sub-Atlantic belt: this forest extends down to mixed broad-leaved oak forests (1300-800 m a.s.l.) and then to the low-altitude (800-50 m a.s.l.) mixed evergreen oak woodlands (Erico-Quercion ilicis) of the Mediterranean belt. Evergreen woodland is dominated by cork oaks (*Q. suber* and/or *Q. ilex*), often intermingled with broad-leaved oaks (*Q. virgiliana*, *Q. amplifolia*, and *Q. delechampi*), ashes (*F. ornus*), and pines (*P. pinea*). The undergrowth layer is mainly composed of *Erica arborea*, *Arbutus unedo*, *Cistus creticus*, *C. monspeliensis*, *C. salvifolius*, and

Calicotome infesta. A significant effect of vegetation belt on the number of captured individuals was found. Dormice occurred more in mixed broad-leaved and evergreen oak forests below 800-1300 m a.s.l., than in beech forests at higher altitudes, and avoided coniferous plantations. A preference for mixed oak stands with high connectivity was found. In addition, more logs and litter could contribute to habitation. But dormice did not use forest plots with dense undergrowth.

In the Czech Republic and Slovakia, the diversity of biotopes of the species is associated with a variety of landforms (Anděra, 1986). The dormouse was found rather sporadically among mixed and deciduous forests on the slopes of the lower-middle belt of mountains. The vertical amplitude of the distribution in former Czechoslovakia extends from 150 up to 1300 m above sea level. The maximum appearance is in the range of 200-600 m a. s. l. Beside beech forests, the dormouse was found here in oak and oak-hornbeam forests, screewoods, rocky grasslands, and different ecotone habitats. It also favors geomorphologically diverse territories, e.g. rock walls, caves, sinkholes, screes, etc. According to the survey of distribution by standardized mapping grid in the Czech Republic, the edible dormouse occurrence was significantly positively affected by vertical relief heterogeneity, annual precipitation, an increasing proportion of masting deciduous trees (beech, oak, and maple) in stands, and length of the growing season. The highest probability of dormice presence occurred in the eastern area of the Czech Republic, in the mountain range and its foothills, on the border with Slovakia. Further areas with high occurrence probabilities were in NW Bohemia and the mountain range bordering Bavaria, Germany (Adamík et al., 2019).

Nest box studies in Northern Moravia showed that dormice live there in a broadleaved deciduous forest with the admixed coniferous forest at the elevation of 650 to 950 m (the valley of the Merta Creek, Vernířovice) and the beech forest with little developed shrub and herb strata (State Nature Reserve “Pod Trlinou”, Lesnice) (Gaisler et al., 1977). One of the study sites (near Dlouhá Loučka) represented a mosaic of managed mixed forest stands with an average age of 90 years and with the dominant tree species sessile oak and European beech (Holcová Gazárková & Adamík, 2016).

Dominating of coniferous species in biotopes of the edible dormouse was noted for studies in Poland. One of them in the center of the country was conducted in Kozienice Landscape Park (Iwińska et al., 2020). In the study area Scots pine (77%), silver birch (11%), sessile oak (9%), and hornbeam (2%) formed the canopy. It also included an admixture of spruce, small-leaved lime, sycamore maple, Norway maple, and aspen. The secondary layer of the forest was formed by young hornbeam, spruce, and black locust. In south-eastern Poland, Małopolska Voivodeship Landscape Park Complex, in the Carpathian Mountains, the dormouse inhabits mainly fir, beech, and beech–fir forests rich in fruiting plant species (Fedyń et al., 2020).

Also, coniferous tree species were noted in dormice habitat in the reserve Belovezhskaya Pushcha (Belarus), where it is two-tiered stands dominated by spruce, oak, less often hornbeam, ash, and

maple. In most cases, these are old-growth stands with a large number of old stumps and deadwood. Rich undergrowth (spruce, hornbeam, oak, ash, less often maple and birch) and bush (hazel, euonymus, February daphne (*Daphne mezereum*) are common (Pivovarova, 1956). One of the recent finds in Belarus was made in a dense spruce-deciduous forest with developed undergrowth (Krapivko, 1999).

On the east of the European plot, in the territory of Russia, the number of dormice is extremely low, and the range is represented by individual local finds. In the forests of Bryansk Oblast (Russia), where the species was found, pines were comparatively common, forming forests of a mixed type. In Moscow Oblast, on the left bank of the river Oka, a litter of dormice was found in a birch forest (Ognev, 1947). In the Ryazan Oblast, the dormouse was found in a pine-broad-leaved forest on the right bank of the river Pra (Borodina, 1960).

Biotopes in the vicinities of the Volga river. Most of the habitats in this plot include broad-leaved and mixed forests with oak and secondary communities. In Nizhniy Novgorod Oblast during the nestbox study, the dormice were found in the forest with the predominance of small-leaved lime and Norway maple and admixture of pedunculate oak, European white elm (*U. laevis*), rowan, silver birch, aspen, goat willow (*Salix caprea*), spruce, Scots pine, with undergrowth consist of hazel and bird cherry (Krivonogov et al., 2019).

Currently, *G. glis* inhabits the coniferous and broadleaved forests of Mordovia (Andreychev, 2020). In the Republic of Tatarstan, the dormouse is relatively common in the riverside pedunculate oak forests of the Volga right bank, from the confluence of the Sviyaga river to the south. Its main habitat in Tatarstan is the forests on the Volga slopes, formed by small-leaved lime and pedunculate oak with a significant admixture of maple, hazel, elm, and aspen. On the rocky slope of the Volga banks, the dormice live in the crevices of the rocks. Two young dormice were found on the slope of the Volga terrace in blackberry thickets (Popov, 1960).

In Penza oblast, the dormouse was found mainly in watershed and floodplain broad-leaved and coniferous-broad-leaved forests, as well as in walnut-fruit plantations (Ilyin et al., 2006).

Further south along the Volga, the dormouse lives in the Zhiguli Mountains (Vekhnik, 2020). The spectrum of forest biotopes inhabited by dormice there includes forests dominated by pedunculate oak, small-leaved lime, Norway maple, silver birch, Scots pine, and aspen. The maximum abundance of the species was recorded annually in different biotopes. The number was the highest in the old-growth floodplain oak forest with a well-developed undergrowth of goat willow, European spindle, bird cherry, maple, hawthorn, blackthorn, and kalina (*Viburnum* sp.). Also, a permanently high number of dormice is observed in the old-growth oak-maple-lime forest with an

admixture of birch and maple with dense hazel undergrowth. The presence of undergrowth here is of decisive importance in the distribution of dormice.

Biotopes in the Caucasus-Asian plot. The habitats of the dormouse in this area gradually pass from the abundantly populated Ciscaucasia and the Caucasus Mountains along the Asian territory to single finds on the border of the species-area in Turkey and Iran. This part of the distributional range includes the most variable tree composition, including several oak and beech species, various fruit and nuts-bearing trees.

In the Caucasus, the dormouse inhabits the forest belt of the Main Ridge of the Caucasus, from the Ciscaucasian steppes and the Black Sea coast to the upper limit of arboreal vegetation (Zharkov, 1971). The dormouse lives here in most of the forests and gardens, being especially numerous in the lower zone of mountain forests and the foothills of the Krasnodar Territory, Abkhazia, Adjara, Azerbaijan, and Dagestan. The main habitat of the dormouse here is lowland forests with an abundance of old hollow trees: oaks, wingnuts (*Pterocarya fraxinifolia*), and willows (Vereshchagin, 1959).

A detailed description of biotopes is given for the Caucasus Reserve in the first half of the last century (Donaurov et al., 1938). As far as it is still reserve territory, it should be actual nowadays. The main habitat of the dormouse in the Caucasian Reserve is broad-leaved forests. The belt of deciduous forests is located up to 800-1200 m above sea level. The main tree species are oaks (*Q. hartvissiana*, *Q. sessilifolia*, *Q. robur*), oriental beech, hornbeam, and maples (*A. pseudoplatanus*, *A. tataricum*, *A. platanoides*). In the southern slopes also sweet chestnut (*Castanea sativa*) grows. This belt is divided into two zones: a subzone of oak (before 800 m) and a subzone of beech (upper 800 m). Also, some fruit trees and plots of fields being previously parts of gardens are present.

Dark coniferous forests with an abundant admixture of beech and hazel are also inhabited by the dormouse. The belt of dark coniferous forests lies from 800-1200 to 1700-1900 m a.s.l. This area includes Nordmann fir (*A. nordmanniana*), and oriental spruce (*P. orientalis*), with a considerable admixture of oriental beech and other broad-leaved species. Sometimes the dormouse occurs in the scaffolding upper forest belt, including downy birch (*B. pubescens*), red-bud maple (*A. trautvetteri*), oriental beech, and others, habiting before the last beech trees. The maximum number of dormice is found in continuous plantations of fruit trees and beech forests with an admixture of oak and other species (Donaurov et al., 1938).

In Georgia, dormice are numerous in beech or, more rarely, oak forests (Papava, 1939, cited from Ognev, 1947). They are widespread in Talysh and Lankaran, starting from the seashore, and reaching the upper border of the forest from 600 to 1800 m above sea level (Kadatskiy, 1964). The mammals are found mainly in the mountain-forest region, to a lesser extent – in the gardens of the Lankaran lowland and separate forest areas along the upper border of the forest. Occasionally found

in the mountain-steppe region among rocks with rare thickets of oriental oak. The largest numbers are reached in the mixed deciduous forest of the Hyrcanian type, in summer and autumn – in walnut gardens. In Adjara, the species is found in forests with a predominance of beech, oak, common walnut, and wild fruit trees (Alania et al., 1971).

In the Talysh mountains (territory of Azerbajdzhan) the biotope was considered the most suitable for the edible dormouse in the Caucasus (Spangenberg, 1935). The biotope was situated in the foothills and on the lowlands bordering them, up to 700 m a.s.l. Dry forests included various fruit trees, Persian ironwood, chestnut-leaved oak (*Q. castaneifolia*), hornbeam, and others. In the southern parts of the region, on the eastern slope of Talysh, the mixed forest acquires a subtropical character. Along with the old trees entwined with wild grapes (*Vitis coignetiae*), ivy (*Hedera helix*), lianas, and other climbing plants, herbaceous and shrubby vegetation was highly developed. In some places there were groves of mimosa (*Albizia julibrissin*). Higher in the mountain forests, which start at 700 m and border the upper treeless belt of mountains, the vegetation was poorer. Up to an altitude of 1000 m a.s.l. the forest consisted of chestnut-deciduous oak, beech, maple, and hornbeam. Above 1000 m, where the forest mainly consisted of Caucasian mountain oak (*Q. maorauptera*) and field maple (*A. campestre*) and only in some places small groves of beech were mixed with it, the number of dormice was lower.

In the Vartashen region of Azerbaijan, the dormouse lives in lowland and mountain forests, rising to the border with alpine meadows (2000 m above sea level). It is found in large quantities in fruit and nut orchards (Meyer & Scholl, 1955). In Armenia, the dormouse lives mainly in deciduous and mixed forests, as well as in orchards located near the same forests (Sargsyan & Yavryanya, 2019).

In Iran, the dormouse prefers deciduous woodland at a relatively low elevation along the southern coast of the Caspian Sea. The vertical range does not exceed 980 m a.s.l. In northern Iran, rodent damages the olive cultivations (Gharkhloo et al., 2021).

Vahidi et al. (2017) studied habitat fidelity in the Hyrcanian forests (northern Iran) using a direct spotlighting method. The main factors were the presence of food items and the connectivity of the tree canopy. Naderi et al. (2016) made niche-modelling there. Vegetation consists of oriental beech, hornbeam, Manna ash (*F. ornus*), oriental wild apple (*Malus orientalis*), various *Prunus* spp., wild grapevine (*Vitis sylvestris*), common buckthorn (*Rhamnus catharetica*), black alder (*Alnus glutinosa*), common fig (*Ficus carica*), Caspian locust (*Gleditsia caspica*), and chestnut-leaved oak. Temperature seasonality (18.6%), slope (16.9%), distance to forest patch dominated by oaks and oriental beech (13.9%), and mean temperature of the coldest quarter (10.4%) were the most important variables. Further study by Ahmadi et al. (2018) showed the differences in amounts of precipitation and thermal variability between habitats of *Glis* genetic lineages in the Hyrcanian forests.

In Turkey, the edible dormouse is tied to humid deciduous and mixed forests (Selçuk et al., 2012). In Thrace, these include stands of oriental beech, Turkey oak (*Q. cerris*), downy oak (*Q. pubescens*), hornbeam, and phillyrea (*Philyrea latifolia*) (Kryštufek & Vohralik, 2005).

Anthropogenic influence on the dormouse distribution

The influence of man on the distribution of the dormouse is controversial: if the ancient peoples contributed to their resettlement, then modern anthropogenic changes in the area caused its fragmentation. The occurrence of the edible dormouse on Salina (Eolian islands) could be explained by deliberate importation by the ancient Romans (Cristaldi & Amori, 1982; 1988). According to the local people in Salina, the edible dormouse occurs only in the areas covered by ancient chestnut-tree cultivations. The populations in Corsica and Sardinia were also introduced by man (Carpaneto & Cristaldi, 1994).

But nowadays, wide portions of once-forested territory have been destroyed by human activities and urbanization. As a result, the habitat has been reduced to a series of small forested woodlots interspersed with wide areas unusable by dormice (Capizzi et al., 2003). Genetic studies showed that the isolation of different populations of edible dormice and their progressive genetic differentiation might have been due to a combination of climate change and increasing human impact on the landscape, starting soon after the Neolithic switch to farming practices. The latest phase of differentiation seems to have occurred during Medieval times (Michaux et al., 2019). This can lead to a decrease in density and loss of genetic diversity (Herdegen et al., 2016). In some cases, sites that might look suitable today carry the historical burden of past habitat destruction which led locally to population extinctions (Adamík et al., 2019).

When analyzing the present distribution and previous finds, it is obvious that despite the edible dormouse is reducing the distributional range in several countries (Pilāts, 2003; Juškaitis & Augutė, 2015), in other countries (Great Britain, Vladimirskaya Oblast in Russia), the species increases its area. In some studies, dormice were found in the original places of deciduous forests changed by anthropogenic activity. For example, in north-western Romania (Ghiris forest, Transylvanian Plain) modern studies were conducted in the forest dominated by field maple and European hornbeam and invaded by locust trees, where previously pedunculate oak and Tatarian maple grew (Sevianu & David, 2012). In North-eastern Bulgaria (Shumen District) dormice for studies were trapped in forest shelterbelt near alfalfa (*Medicago sativa*) fields in the agricultural region (Markov, 2012).

In some countries, the dormouse is considered a pest (Czech Republic, Great Britain; Adamík, 2017). At the current low intensity of dormice studies, it is impossible to determine the trends in abundance dynamics of the species. Also, wide population genetic studies are needed to reveal the influence of the fragmentation of biotopes on the genetic stability of the species.

At present in Poland, the reintroduction of dormice is implemented. The programs are realized in Sierakowski Landscape Park, Szczeciński Landscape Park, and Barlinecko-Gorzowski Landscape park (Jurczyszyn et al., 2002; Jurczyszyn & Łukomski, 2008; Czapracka et al., 2011; Jurczyszyn et al., 2018). Probably, in deeper studies, such programs are required in other countries.

Conclusion

The current distribution of the edible dormouse illustrates its connection with tree species of the Fagaceae family. But even though the dormouse's attachment to deciduous and mixed-deciduous forests is justified by its specialized ecological niche, in many cases the species exhibits sufficient flexibility in the choice of habitats. Researches show that the spectrum of its habitat goes far beyond the typical ones, including broad-leaved tree species. This is often associated with both the proximity of the location of optimal habitats, the growth of derived species, and the adaptability to new ecological conditions. This is especially noticeable when considering habitat fidelity at the boundaries of the range and high-altitude distribution. The descriptions of the species' habitat in different regions are a variegated mosaic of typical and atypical habitats. Such transition is particularly expressed in the altitudinal direction in mountainous regions. The habitation of the species in a particular area often depends on the current or past anthropogenic activity.

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