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Populations of *Muscardinus avellanarius* in north-western Europe can survive in forest poor landscapes, when there are enough hedges (Rodentia: Gliridae)

Populace plšíka lískového (*Muscardinus avellanarius*) v severozápadní Evropě mohou přežívat v krajině chudé lesy, mají-li dostatek křovin (Rodentia: Gliridae)

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Abstract. The hazel dormouse (*Muscardinus avellanarius*) is a strictly arboreal species. In its European lowland range, the forest coverage was heavily reduced during historical times, e.g. down to ca. 4% in the northern German federal state of Schleswig-Holstein in the 18th century. This low forest cover remained for 200 years. According to habitat models, hazel dormice cannot survive in the long-term in habitats with low levels of forest cover (<5–10%). To answer the question, how hazel dormouse populations survived in almost deforested areas the recent species distribution map for north-west Europe was analysed with a GIS-overlay of different habitat data. Additionally, historical maps for north-west Germany were analysed to find crucial historical landscape elements. The history of a site apparently influences the present status of hazel dormice. Forest cover of younger woodlands is still of importance but less determinant. Habitat tradition and continuity are important for habitat suitability for the hazel dormouse and identifying historical hedgerow systems and historical woodlands can help to find places with hitherto unknown presence of hazel dormouse. Apparently, for the hazel dormouse the lack of forest habitats in north-western Europe was successfully compensated by the creation of a hedgerow network. Hedgerows function as a habitat by themselves, not just as a connecting structure. A density of 50 m continuous high quality and well-connected hedgerows per hectare seems to be a minimum for the survival of hazel dormice in north-west European landscapes. The preservation of ancient habitats and the restoration of new habitats as core habitats and connections is a key strategy to facilitate the long-term survival and re-colonisation of species.

Key words. Hazel dormouse, landscape history, isolation, hedgerows.

INTRODUCTION

The hazel dormouse (*Muscardinus avellanarius*) is described as an arboreal woodland species (e.g. Ajrapet’ânc 1983, Bright & Morris 1996, Rossolimo et al. 2001, Juškaitis 2014). It is known that hazel dormice also live in hedges (Hurrell & McIntosh 1984, Eden et al. 1999, Bright & MacPherson 2002, Bright et al. 2006, Wolton 2009, Ehlers 2012). However, a model by Mortelliti et al. (2011) showed the importance of forests for the species. His model

This contribution has been presented at the 10th International Dormouse Conference held at the University of Liège, Belgium, on 11–15 September 2017 predicts that even high densities of hedgerows (30 metres per hectare) are unlikely to increase the probability of occurrence of hazel dormouse in landscapes where there are low levels of forest cover (<5%–10%) and in such low-forested landscapes hazel dormice cannot survive in the long-run, no matter how well the remaining habitat patches are connected (Mortelliti et al. 2011).

In parts of north-western European lowlands, the forest coverage fluctuated widely during historical and recent times due to intensive human impacts on the landscapes. For example, in the northern German federal state of Schleswig-Holstein, the minimum of forest cover of approximately 4% was reached around 1780 (Hase 1983). From then on afforestation has led to 11% forest cover in 2017. However, the period with a forest cover of less than 10% lasted at least 200 years. How did hazel dormouse populations

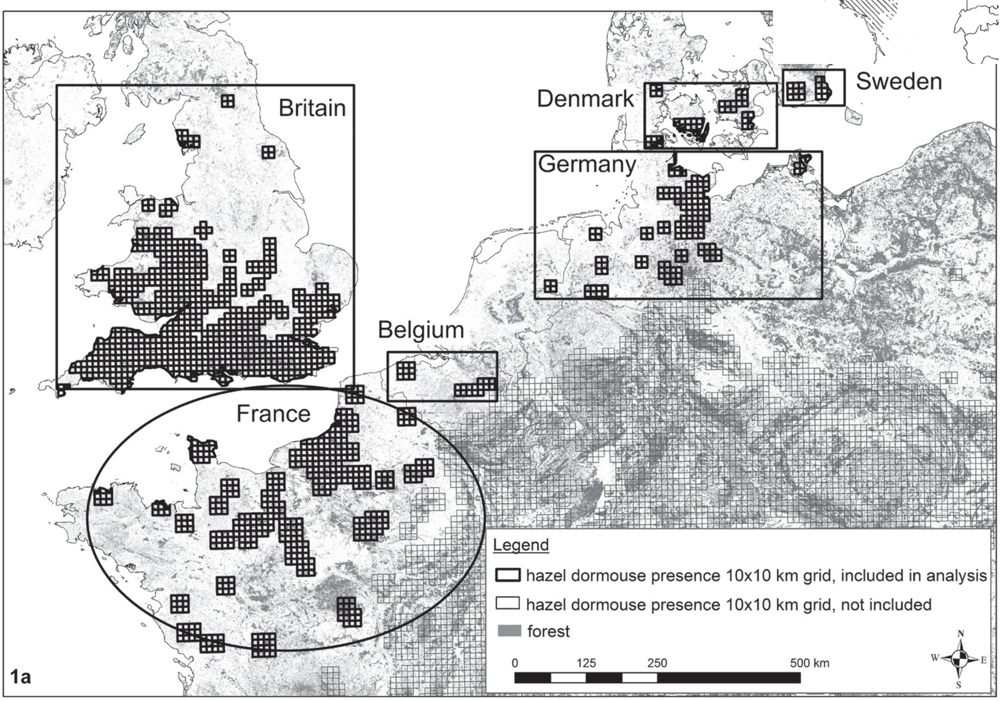

Fig. 1. Study area in the north-western European lowland: a – with hazel dormouse distribution (data provided by the European Environment Agency); b – with distribution of hedge dominated landscapes (Jessen 1937).

Obr. 1. Sledované území nížin severozápadní Evropy: a – s vyznačním rozšíření plšíka lískového (údaje poskytnuté Evropskou agenturou životního prostředí) [Legenda: tučně ohraničené čtverce = čtverce 10×10 km s výskytem plšíka, zahrnuté do analysy; tence ohraničené čtverce = ostatní čtverce s výskytem plšíka; šedé plochy = lesy]; b – s vyznačením rozšíření krajiny s převládajícími keřovými porosty (Jessen 1937).

Table 1. Forest coverage per country and number of raster cells with hazel dormouse presence; forest cover = forest cover of the total country; mean forest cover = actual mean forest cover in the dormouse populated lowland grids; number of grid cells = number of grid cells with hazel dormouse presence in lowland range
Table 1. Pokrytí lesem a počet čtverců s výzkytem plšíka lískového with hazel dormouse presence; pokrytí lesem = pokrytí lesem z celkové rozlohy; průměrné pokrytí lesem = skutečné průměrné pokrytí lesem v nížinných čtvercích s výskytem plšíka; počet čtverců = počet čtverců s výskytem plšíka v nížinném areálu

country / stát	forest cover / pokrytí lesem [%]	mean forest cover / průměrné pokrytí lesem [%]	number of grid cells / počet čtverců
Belgium / Belgie	23	31	71
UK / Spojené království	12	11	710
Denmark / Dánsko	14	14	48
France / Francie	31	18	466
Germany / Německo	33	21	137
Sweden / Švédsko	69	21	20
Schleswig-Holstein / Šlesvicko-Holštýnsko			
1800	4	8	unknown / neznámý
2000	11	14	69

survive in northern Germany during two centuries of deforestation? The situation in northern Germany is typical for many regions in the lowlands of north-western Europe. Here, a high proportion of dormouse populations are isolated from others and the forest cover is much lower than in the central European core populations. We believe, with our investigation in those habitats at the limits of both suitability and extinction, we can learn a lot about the limits of landscape suitability for hazel dormice.

STUDY SITES AND METHODS

The study areas are the north-western European countries at the border of the hazel dormouse range (Fig. 1a) that are well known for their richness of hedgerows (Fig. 1b). More detailed and historical data were available to us for Schleswig-Holstein, the northernmost German federal state. Therefore, special attention was given to the situation there and additional analyses were run for this region. Furthermore, a small field test of results obtained from the various GIS-analyses was conducted at the western part of Mecklenburg-Vorpommern adjacent to Schleswig-Holstein (Fig. 2a).

Data for hazel dormouse distribution are available from the EEA (2014), compiled as part of the Habitats Directive – Article 17 reporting process. We used the dataset of the reporting period 2007–2012. In total, the hazel dormouse was reported for 1,590 grid cells of 10×10 km in the study areas (Table 1).

The programme ArcGIS 10.5.1 was used for the analyses of a GIS-overlay of the hazel dormouse raster-cells with different habitat data. We took raster data of the georeferenced European forest map (Päivinen et al. 2001, Schuck et al. 2002, Kempeneers et al. 2011) and, additionally, for Schleswig-Holstein the polygon-data of old and young forest stands (forest was present / was not present in maps from approximately 1800) (Glaser & Hauke 2004) and polyline-data of recent hedges from official Schleswig-Holstein geodata administration. In the first step, the raster data were clipped for the study site (spatial analyst routine "extract by polygon") in order not to exceed the maximum file size for the GIS

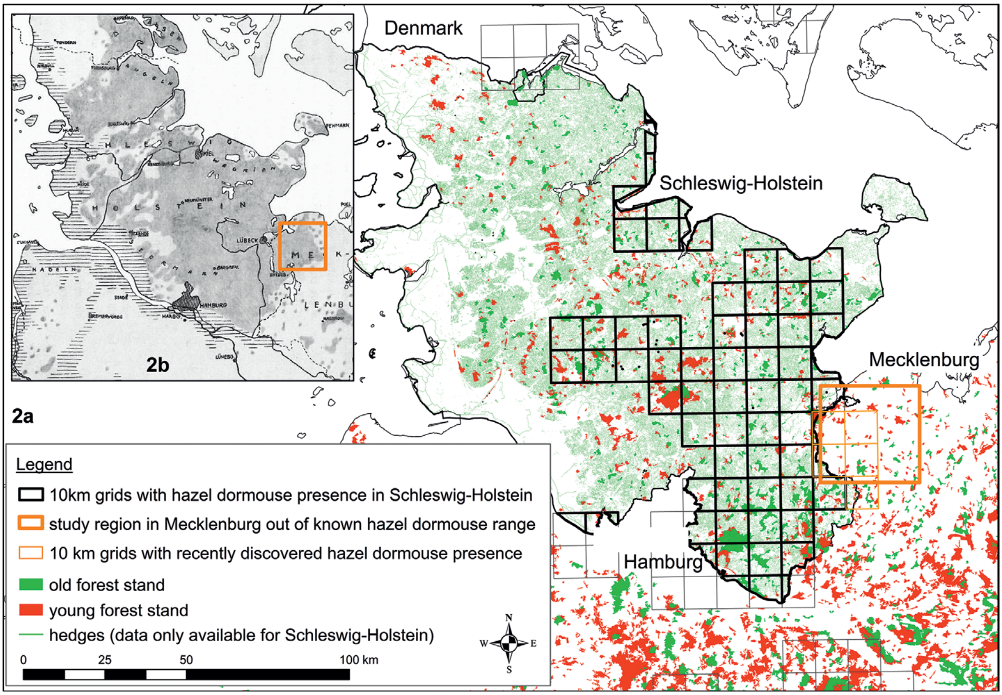

Fig. 2. Study area in northern Germany; a – hazel dormouse distribution and landscape characteristics (old and young forest stands, hedges); b – distribution of hedge landscapes (dark grey = hedge landscape, light grey = hedges without a hedge tradition; Jessen 1937) as a basis for the selection of a study site outside of the known hazel dormouse range in the federal state of Mecklenburg-Vorpommern.
Obr. 2. Sledované území v severním Německu; a – rozšíření plšíka lískového a charakteristik krajiny (staré a mladé lesní porosty, keře) [Legenda: tučně černě ohraničené čtverce = čtverce 10×10 km s výskytem plšíka ve Šlesvicku-Holštýnsku; tučně oranžově ohraničené čtverce = sledovaná oblast Maklenburska mimo areal plšíka; tence oranžově ohraničené čtverce = čtverce s nově dokumentovaným výskytem plšíka; zelené plochy = staré lesy; červené plochy = mladé lesy]; b – rozšíření keřových krajin (tmavě šedá = keřovitá krajina, světle šedá = keře bez keřové tradice; Jessen 1937) jako základ pro výběr sledované lokality mimo známý areál rozšíření plšíka lískového ve spolkové zemi Meklenbursko-Přední Pomořany.

programme. Then we transferred the files from raster data (tiff-format) to polygon data using the ArcMap conversion tool “raster to polygon”. Then we conducted the “union” routine to combine the forest cover data with the hazel dormouse grid data and their attribute tables and finally “merged” all tiles to a single shape including all relevant data in 1.3 million different polygons. Additionally, 697,666 polylines were analysed for Schleswig-Holstein, making a total of 86,329 km of hedges in this federal state. We exported the attribute table files as dbf data to Excel and used “pivot tables” to analyse the dataset. The different probabilities of presence and absence of the hazel dormouse in relation to environmental features were tested for significance by using the online Mann-Whitney-U-Calculator on www.socscistatistics.com.

To verify the GIS-analysis and the hypothesis of the importance of historical landscape elements, we used the maps to predict and detect unknown hazel dormouse populations. We chose a large-scale study site (approximately 30×28 km) outside the known hazel dormouse distribution, representing the eastern limit of the hedge-range according to JESSEN (1937). By checking historical (WIEBEKING 1786, SCHMETTAU 1788) and recent maps (Fig. 5), hedges were identified that were part of the historically dense hedge-system (Fig. 2b). By looking for free hanging summer nests a group of 5–8 skilled (re)searchers investigated several kilometres of hedges and additional forest edges for hazel dormouse presence during late autumn in the years 2007, 2010, and 2012–2017.

RESULTS

The average forest cover in the north-western European countries varies from 12% (UK) to 69% (Sweden) (Table 1). However, the average data for the whole countries do not apply for all regions and there was a dynamic change over the time

Apart from Belgium, the hazel dormouse is present in parts of the countries where the median actual forest cover is even lower than in the country's average. The recent forest cover within the hazel dormouse range varies from 8% in Britain to 27% in Belgium. Again, apart from Belgium, in the lower quartile of grid cells the forest cover is only 10% or lower (Fig. 3). It is very likely that in all regions forest cover was much lower during the past, but for us historical data were only available for Schleswig-Holstein. Here 200 years ago, the forest cover was down to

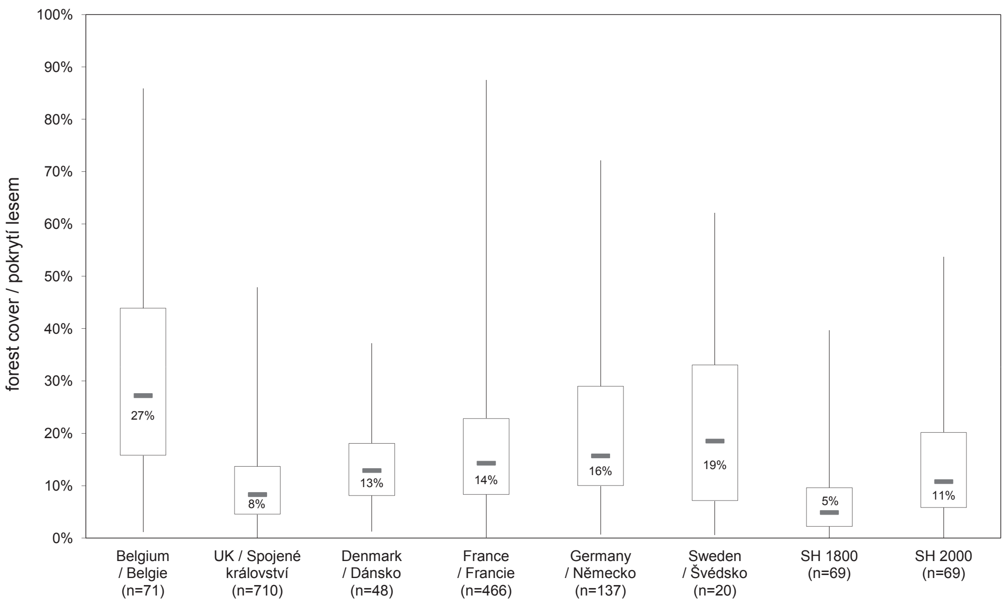

Fig. 3. Forest cover in % of all grid cells with actual hazel dormouse presence (using only grids in fragmented lowland ranges) of the different European countries and in detail of Schleswig-Holstein (SH) in the years 1800 and 2000 (boxplot showing maximum, upper quartile, median, lower quartile, minimum).
Obr. 3. Procentuální pokrytí lesem ve všech čtvercích s přítomností plšíka lískového (použity jsou jen čtverce ve fragmentované nížině) v různých evropských zemích a speciálně ve Šlesvicku-Holštýnsku (SH) v letech 1800 a 2000 (krabicové diagramy vyznačují hodnoty maxima, horního kvartilu, medianu, dolního kvartilu a minima).

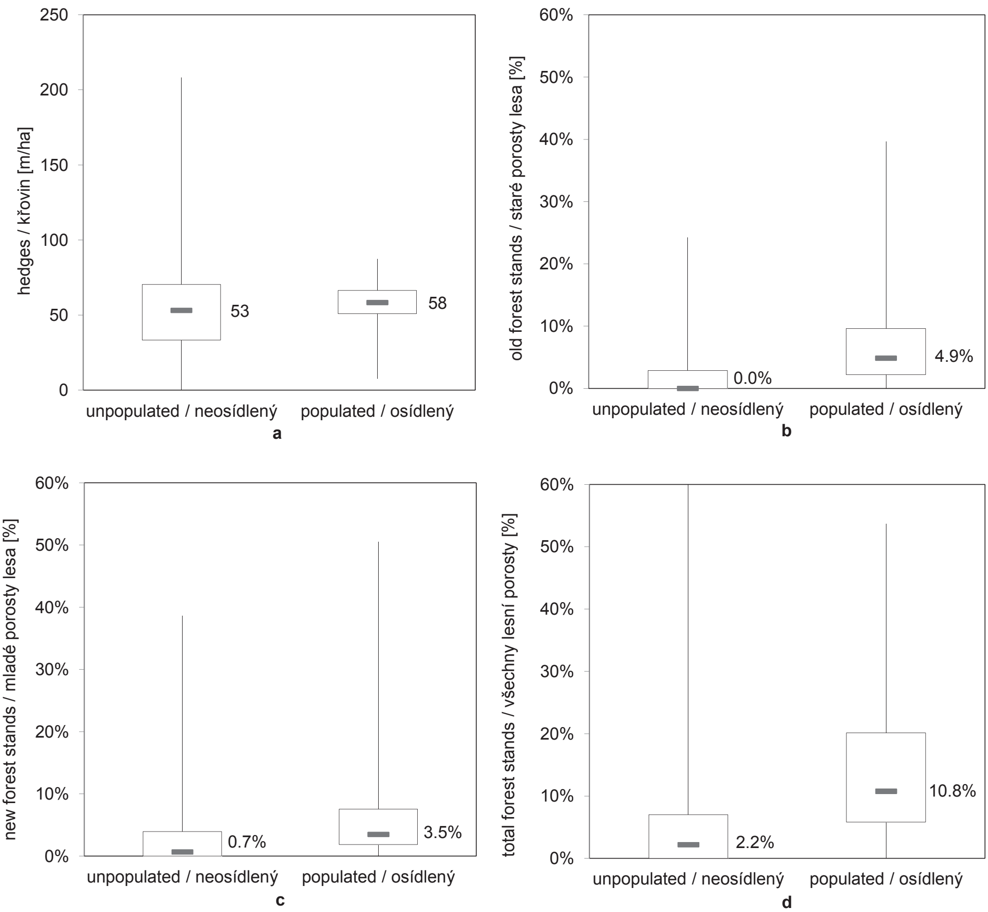

Fig. 4. Some characteristics of 10×10 km grid cells unpopulated (n=145) and populated (n=69) by hazel dormouse in Schleswig-Holstein (boxplots showing maximum, upper quartile, median, lower quartile, minimum are presented): a – recent hedge density (n.s.); b – density of old forest stands ($p<0.001$); c – density of new forest ($p<0.01$); d – density of total forest stands ($p<0.001$).
Obr. 4. Něco charakteristik čtverců 10×10 km neosídlených (n=145) a osídlených (n=69) plšíkem lískovým ve Šlesvicku-Holštýnsku (krabicové diagramy vyznačují hodnoty maxima, horního kvartilu, medianu, dolního kvartilu a minima): a – současná keřová hustota (n.s.); b – hustota starých lesních porostů ($p<0,001$); c – hustota nových lesů ($p<0,01$); d – hustota celkových lesních porostů ($p<0,001$).

4%. It is apparent that hazel dormice can survive in very forest-poor landscapes with less than 10% forest cover, even down to 4%.

The hazel dormouse is present in 69 grid cells and absent in 145 cells in Schleswig-Holstein. The forest cover here is comparatively low, both in recent (11%) and historical times (4% in

1800). Today, the grid cells with hazel dormice presence are characterised by a significantly higher forest coverage (median 10.8%) than those without hazel dormice (median 2.2%) (Fig. 4d).

The history of a site apparently influences the present status of hazel dormice. Where no ancient woodland remains, there is only a small chance of hazel dormice being present today (Fig. 4b). But if even small patches of forests have been left in the past, the likelihood of surviving hazel dormouse populations is high. The difference is highly significant. When looking at younger forests, the difference is smaller but still significant (Fig. 4c). Where hazel dormice are present today, a median 3.5% of the landscape has been re-afforested since 1800. In places where it is absent, nearly no afforestation has taken place (0.7%).

There is no significant difference in hedge density between populated and unpopulated grid cells. There are 53 metres of hedges per hectare in grid cells with hazel dormice present and 58 metres of hedges per hectare in cells where hazel dormice are absent (Fig. 4a).

Knowledge about ancient woodland and historical hedgerow systems can help to identify places with potential presence of hazel dormice. According to Jessen (1937), the hedgerow--dominated landscape extended from Schleswig-Holstein into the western parts of neighbouring Mecklenburg (Fig. 2b). Detailed historical landscape maps given by Wiebeking (1786) and Schmettau (1788) show a dense hedgerow network with small and scattered woodlands. Some of the ancient hedges and woodlands still are present today (Fig. 5). In this section of our study area, we found eight places with one or more hazel dormouse nests. All records were found in woody structures which were already present in the 18th century and remained until today. In the wider study region, we found hazel dormouse evidence in four 10 km-grids, where this species was completely overlooked in the past (Fig. 2a) (Büchner 2012). No hazel dormouse nests were found in the eastern and southern neighbouring grids representing landscapes beyond the range of hedges, even though they were repeatedly investigated between 2007 and 2017.

DISCUSSION

This study relies on grid data submitted by the Member States of the European Union to the European Topic Centre on Biological Diversity. One should have in mind that transferring point data into grid data will cause blurring and additionally some states like Germany for example, reported the data according to a different grid system which had to be re-calculated for the 10-kilometre squares. However, we believe that the data set with hazel dormouse records for 1,590 grid cells is robust enough for an analysis of habitat data at that scale.

The results of this study clearly show that habitat tradition and continuity is an important factor for present-day habitat suitability for the hazel dormouse. Our results from Schleswig--Holstein compare favourably with the data of Bright et al. (1994), who found hazel dormice more frequently in ancient woodland than in recent woodland in the UK. It can be assumed, that this pattern is typical at least for north-western Europe and highlights the importance of ancient woodland as reserves for biodiversity.

Currently, hazel dormice are scattered but relatively widespread throughout north-western Europe, but ancient woodland was reduced to small copses in most parts of the study region. For Schleswig-Holstein, we can state that there are only few parts of the federal state where the habitat suitability today is high (Dietz et al. 2018) and recent evidence of hazel dormice is lacking. Hazel dormice have survived in spite of the relative lack of forests (4%) due to a high density of hedges locally. The density of hedges was on average 115 metres hedgerow per hectare

Fig. 5. Maps of study site outside the known hazel dormouse distribution range in the federal state of Mecklenburg-Vorpommern: a – historical landscape map by Wiebeking 1786.
Fig. 5. Mapy sledovaného území mimo známý areál rozšíření plšíka lískového ve spolkové zemi Meklenbursko-Přední Pomořany: a – historická mapa krajiny Wiebekinga z roku 1786.

(Müller 2013), meaning a highly suitable habitat. Genetic studies (Mouton et al. 2016) offer proof that dormice did not recently immigrate here but survived from the past.

Studies in England and eastern Germany emphasize a minimum woodland size of 20 hectares for long-term survival of a local population lacking connections to nearby habitat (Bright et al. 1994, Keckel et al. 2012). There is a high risk of extinction in small and isolated sites (Bright & Morris 1996). According to Bright & Morris (1996), hedgerows work as corridors between woodlands ensuring the linkage between subpopulations and the long-term survival of the species.

At the landscape scale, Mortelliti et al. (2011) found that probability of hazel dormouse presence was related to the amount of habitat available. In their model, the probability of hazel dormouse presence increased with the amount of forest cover and increasing structural connectivity (hedgerows) in the landscape. The main conclusions of this model are confirmed with the data from the present study. However, for low levels of suitable habitat (values roughly corresponding to 5–10% of forest cover in the landscape as in in our study area), the model by Mortelliti et al. (2011) predicted that even extremely high values of structural connectivity will have little effect on probability of presence. Apparently, for the hazel dormouse the lack of forest habitats in north-western Europe was successfully compensated by the creation of

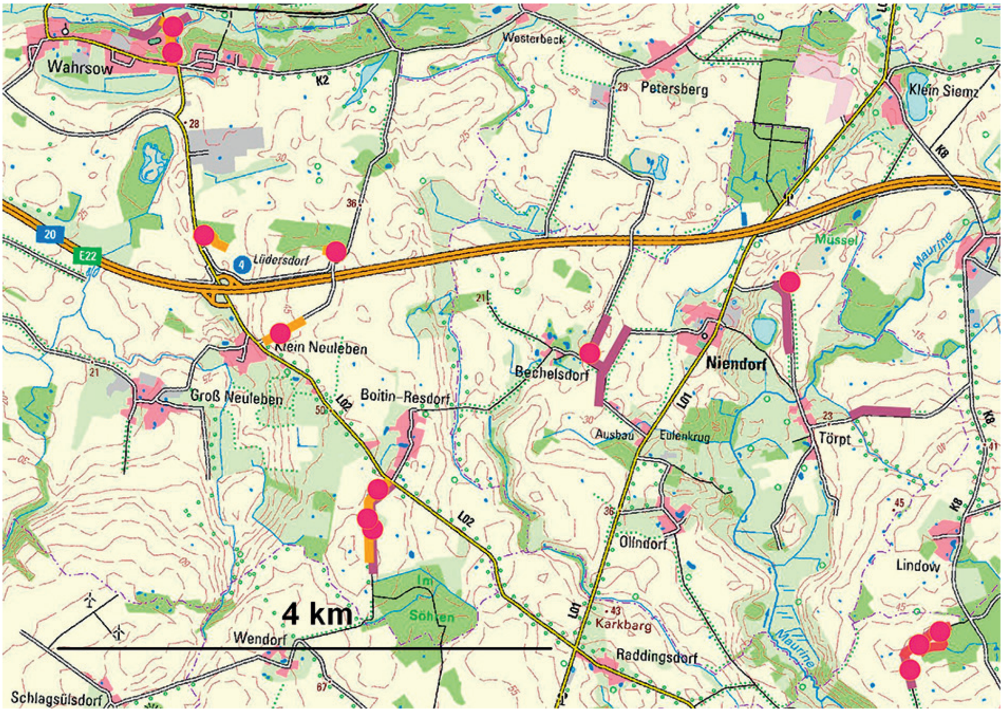

Fig. 5. Maps of study site outside the known hazel dormouse distribution range in the federal state of Mecklenburg-Vorpommern: b – recent map (OpenStreetMap 2018). Dots represent the position of free-hanging hazel dormouse summer nests detected in November 2016.

Fig. 5. Mapy sledovaného území mimo známý areál rozšíření plšíka lískového ve spolkové zemi Meklenbursko-Přední Pomořany: b – současná mapa (OpenStreetMap 2018). Červené kroužky představují lokality volně zavěšených letních hnízd plšíka lískového nalezených v listopadu 2016.

a hedgerow network. We are confident, that hedgerows function as a habitat by themselves, not just as a connecting structure.

The hedgerow network in Schleswig-Holstein and adjacent regions had to be developed after different land use acts from the early 18th century onwards (Jessen 1937), but was basically already present in the decades or even centuries before (Müller 2013). In the late 18th century at the time of the heaviest loss of forests, the hedgerow network reached its maximum with a density of >110 metres per hectare in certain regions of northern Germany. It is now reduced to little more than 50 metres per hectare. Our hypothesis is that the dormouse can survive in almost completely deforested landscapes if the density and quality of the hedge-system are sufficient. A density of 50 metres of high-quality hedgerows per hectare seems to be a minimum for the survival of hazel dormice in the landscapes of north-west Europe. From our own data we cannot prove the importance of the connectivity of hedges for dispersal, but we are convinced that connectivity plays an important role.

Understanding the historical dynamics of habitats may be crucial for the interpretation of the historical and recent distribution of not only the hazel dormouse. Analysis of maps of historical and recent habitat distribution can facilitate monitoring and conservation of species. It helps to identify:
(a) possible key factors for the species' long-term survival;
(b) potentially undiscovered populations and
(c) strategies for the regeneration of a favourable conservation status.

Furthermore, it is apparent, that historical development of landscapes and thus population and range dynamics must be considered in modern "species occurrence models", where usually only the recent distribution of species and habitat factors are used. But recent distribution depends not only on recent habitat suitability, but also historical habitat suitability.

Data from the present study also contribute to practical conservation effort. The importance of hedgerows for the conservation of a wide range of species is widely understood and thus the restoration and maintenance are important conservation actions (Bright & MacPherson 2002, Schulz et al. 2013). Hedges for hazel dormice need to be well developed (at least 12 different shrub or tree species are needed according to Ehlers (2012) and Wuttke et al. (2012), be sufficiently high (Bright & MacPherson 2002) and be more or less without gaps (Bright 1998). So, the creation of hedges to benefit the hazel dormouse needs expertise (Bright & MacPherson 2002). As the restoration of a hedgerow network is very costly the effectiveness of any investment should be proved in advance (Davies & Pullin 2006). In Schleswig-Holstein, the practical experience of the Federal State Nature Conservation Foundation is, that it costs approximately 50 € per metre of hedge restoration (including soil excavation and fencing). So, 5 Million € – excluding the land-purchase costs – would be needed to increase the hedgerow density in a single 10 km grid square by 10 metres per hectare. In Schleswig-Holstein, the average density of hedges decreased from around 115 metres per hectare to 50 metres per hectare from 1800 to today (Müller 2013). Thus, the destruction of historical hedge-richness to create modern hedge-poverty means a loss of 32 Million € per 10 km grid square based upon the cost of its restoration. It is unrealistic to re-establish historical hedge densities on a large scale. For the best outcome from the investment of scarce conservation funds it is important to have a precise analysis of historical and recent landscape characteristics. Here especially the preservation of ancient habitats and the restoration of new ones and their connections is a key strategy to facilitate long-term survival and re-colonisation of species (Dietz et al. 2013).

SOUHRN

Plšík lískový (*Muscardinus avellanarius*) je striktně stromový druh. Ve jeho evropském nížinném areálu bylo v minulosti silně sníženo pokrytí lesem, např. v severní německé spolkové zemi Šlesvicku-Holštýnsku na cca 4 % v 18. století, kde pak takto nízké lesní pokrytí zůstalo 200 let. Ovšem podle stanovištní modelace plšík lískový nedokáže dlouhodobě přežívat v biotopech s nízkou mírou lesního pokrytí (<5–10%). Aby bylo možno odpovědět na otázku, jak mohly populace plšíků lískových přežít v téměř odlesněných oblastech, byla aktuální mapa rozšíření plšíka v severozápadní Evropě analyzována pomocí systému GIS s překrytím různých datových vrstev a dále byly analysovány historické mapy severozápadního Německa, ve snaze nalézt v historické krajině rozhodující prvky umožňujíci přežití plšíka. Tradice lokality zjevně ovlivňuje možnost přežívání a současný stav populace plšíků. Pokryvnost mladšími lesy je velmi důležitá, avšak nikoliv určující. Tradice a spojitost biotopů je důležitá pro užití stanovišť plšíky lískovými a identifikace historických systémů živých plotů a historických lesů může pomoci nalézt místa s dosud neznámým výskytem plšíků. Zdá se, že pro plšíky lískové byl v severozápadní Evropě nedo-

statek lesních stanovišť úspěšně vynahrazen vytvořením systémů živých plotů. Živé ploty představují nejenom spojovací strukturu, ale biotop samy o sobě. Hustota 50 m dlouhých, setrvale vysoce kvalitních a dobře propojených živých plotů na hektar se jeví jako minimální podmínka pro přežití plšíka v krajině severozápadní Evropy. Zachování starobylých biotopů a tvorba nových stanovišť jako jádrových biotopů a jejich propojení představuje klíčovou strategii pro umožnění dlouhodobého přežívání a rekolonisaci plšíka lískového i dalších druhů.

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