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The occurrence of the hazel dormouse, *Muscardinus avellanarius*, in the south-western Baltic region and its biogeographical implications

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Abstract. The occurrence of hazel dormice on some islands in the Baltic Sea raises the question about the origin of these long isolated populations. The spread of hazel dormice from their Pleistocene shelters in southern Europe to the north was facilitated by a rapid spread of hazel during the Boreal after 10800 cal. yr BP and subsequently hazel dominated woodlands in central Europe. The immigration of the hazel dormouse from central Germany to Ruegen is not supported by findings and seems to be unlikely due to habitat fragmentation in the north-eastern German mainland. This is indicated by areas of poor sandy soils with poor pine forests besides wide and sandy river valleys and wetlands. In contrast, immigration via Denmark is rather possible considering the post-glacial development of the south-western Baltic Sea region. Especially the Darss Sill could have been used as a land bridge between south-eastern Denmark and north-eastern Germany about 9800 to 8800 cal. yr BP. A further migration of the species towards the east, e.g. to Bornholm, might be prohibited by the existence of the vast Oder River valley.

Key words: island populations, vegetation history, Denmark, Mecklenburg-Vorpommern, Ruegen

Introduction

The hazel dormouse, *Muscardinus avellanarius* (L.), is a rare species in North Germany and Denmark. Its range is restricted and shrinking in some parts (Vilhelmsen 2007). However, it can be found on a few islands in the south-western Baltic Sea area (Fig. 1), e.g. Funen (Fyn), Zealand (Sjælland), Langeland in Denmark (Vilhelmsen 2007) and Ruegen (Rügen) in Germany (Büchner et al. 2002, Büchner 2012). Curiously no hazel dormouse population is known on the German mainland near Ruegen although the island was separated by the sound “Strelasund”, which is several hundreds of meters in width, probably not before the Littorina Transgression at about 6800 cal. yr BP (Lampe et al. 2010). The closest population in Germany occurs at the western border of Mecklenburg, around 200 km away from Ruegen. Populations of hazel dormice known from southern Sweden and Denmark are even closer about 75 and 100 km away, respectively. This distribution pattern raises several questions. Which way did the hazel dormice take to reach the Island of Ruegen and

the Danish islands as well? Other mammals like the red fox, *Vulpes vulpes*, or the stone marten, *Martes foina*, can be observed to cross the frozen sea in harsh winters (Siefke & Schröder 2010). This seems to be impossible for the hibernating hazel dormouse. Nevertheless, three other hypotheses can be proposed to explain the island populations’ occurrence:

1) a translocation of hazel dormice by humans (willingly or accidentally) took place in the past.

2) could the occurrence on the islands in the Baltic Sea be explained by rafting hazel dormice? With the ability to fall into torpor the hazel dormouse seems to be better adapted to such a challenging journey than several other small mammals.

3) temporary land bridge(s) could have allowed an immigration to take place. The hazel dormouse is an arboreal woodland species strictly connected to woody vegetation (Juškaitis & Büchner 2013). Thus, the climatic and edaphic conditions on those land bridges must have allowed suitable woodlands. Furthermore, there must have been a sufficient time span for the hazel dormouse to migrate. Are there

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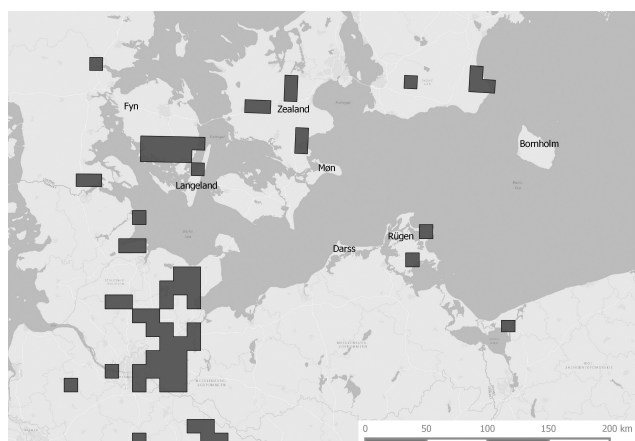


Fig. 1. Distribution of hazel dormice in the southern Baltic (Source: Eionet – European Topic Centre on Biological Diversity, Article 17 consultation species report for 2007 to 2012); remark by the authors of this paper: no proof of the record on the north-west corner of Poland near the German border could be found so far.

evidences for such conditions during the 12000 years after the last glaciation?

The translocation hypothesis

A large population of the edible dormouse, *Glis glis*, exists on the small island Greifswalder Oie in the Baltic Sea south-east of Rügen. It can be traced back to the escapes of a few specimens from a private breeder in 1995 (Siefke & Schröder 2010). The edible dormice rapidly spread in the little forest since then. Garden dormice, *Eliomys quercinus*, temporarily appeared at places in Germany far away from their known distribution. Some cases can clearly be connected with escapes from captivity. Additionally, garden dormice have been proved to be transported by cars or together with building material accidentally (Meinig & Büchner 2012). In principal, this can neither be excluded for the hazel dormouse. There may be breeders and accidental translocations as well. However, there has not been a single indication for these kinds of events with hazel dormice on Rügen so far. On contrary, there are records of the species for Rügen which are 50 years of age and older (Siefke & Schröder 2010). The hazel dormouse can be found on several parts of the island of Rügen, separated by open sounds, huge arable fields and urban areas (Büchner et al. 2002, Büchner 2012). If translocations (or escapes) were an explanation for the occurrence of hazel dormice on Rügen, they should have happened at several places and they should have started at least 100 years ago. Both facts clearly suggest that the hazel dormouse is autochthonous to the island. Similarly, a translocation of Danish hazel dormice by maritime trade during the Viking-age or Hanseatic-era seems to be unlikely.

Rafting on driftwood – a possibility for the hazel dormouse to spread across the Baltic?

Rafting on driftwood is discussed to be a possibility for a passive transport of small mammals. Samonds et al. (2012) describe it as a plausible mechanism for several animal species to successfully migrate to Madagascar. According to Kappeler (2000) entire groups of hibernating lemurs could have survived weeks or even months without food or water staying in torpor in a hollow tree while rafting across the sea. In some regions driftwood is a common phenomenon, e.g. along coasts with mangroves where the trees grow in the shallow sea water or in Siberia where the rivers deliver significant amounts of driftwood to the Arctic Ocean. However, natural driftwood does nearly not occur in the present south-western Baltic Sea. Most of the observed driftwood is marine litter of anthropogenic origin that is completely unsuitable for small mammals rafting. Only nearly complete trees or even small rafting islands could provide a save raft for a journey across the sea. However, a tree as a whole with crown and root is absolutely unsuitable for both, land and water transportation. Root and crown of the tree extend far below the tree barycentre and cause an anchoring effect for the tree on land as well as in shallow waters. Thus, there is always a delay till a fallen tree floats freely and small mammals should have the opportunity to return to land.

Nevertheless, under certain circumstances whole trees become driftwood. Marine driftwood originates from rivers as well as from seashores. But both, the riverine and the coastal environment in the Baltic region, are not appropriate for a rapid tree transport from its growth site into deeper waters. The river mouth areas are usually unsuitable for driftwood passages. They can even work as traps because of sediment accumulation in shallow delta-like water environments.

The coastal zone in the south-western Baltic is frequently affected by high energy events such as storms and floods. Large scale erosion including the transport of trees to the beach can be caused. Generally these events happen during the winter. They are not common in the summer time. Different transport mechanisms are possible for trees, i.e. falling down from the cliff edge, sliding on a cliff slope or transport in a mudflow. But the transport length is always short. Usually it ends on the beach or in shallow waters. The trees remain there until the anchoring extensions of crown and roots are destroyed by the ongoing movement of the waves. After that a new flood is necessary to make the tree free-floating and transport it into deeper water.

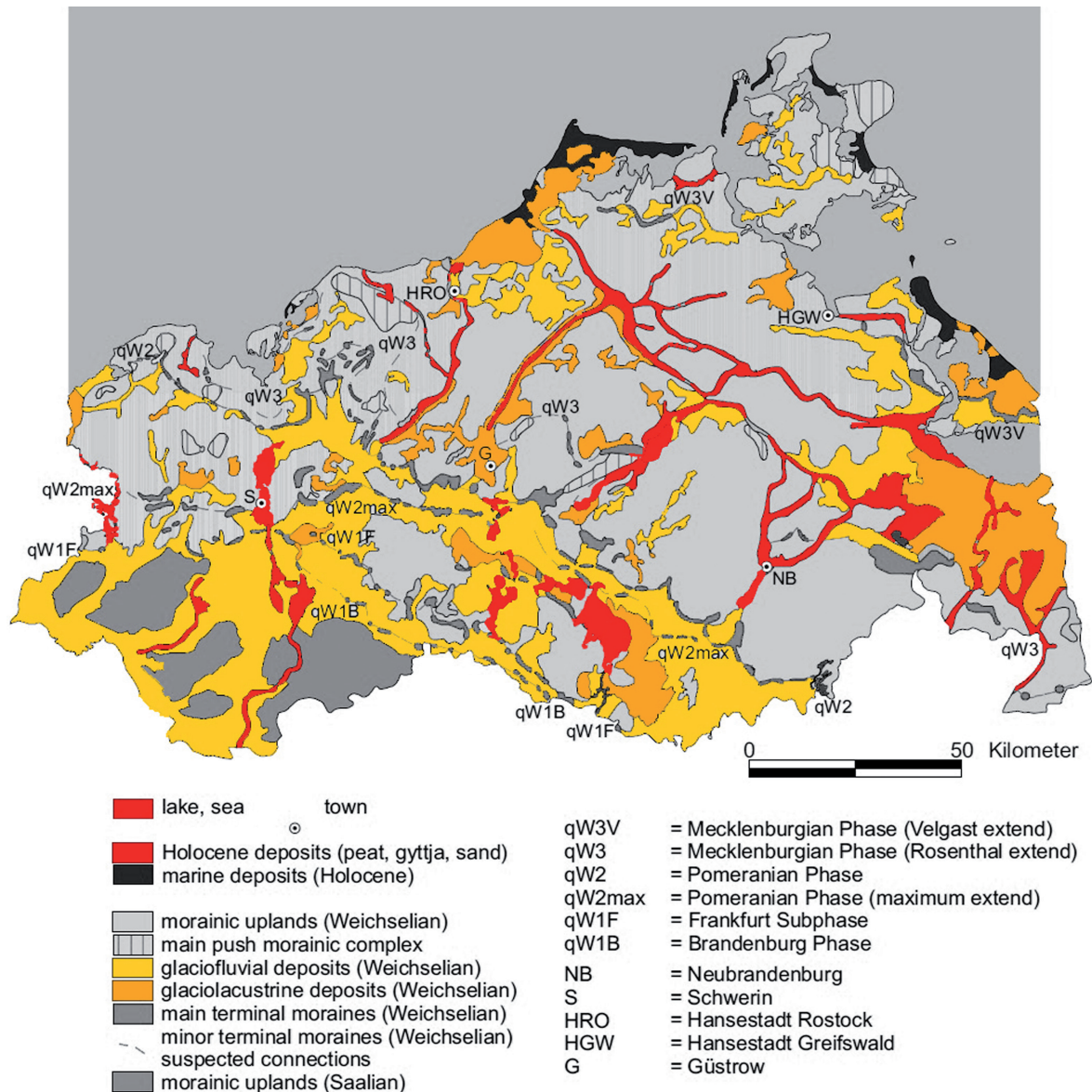


Fig. 2. Quaternary deposits and evolutionary phases in Mecklenburg-Vorpommern (Source: Lampe & Lorenz 2010, modified).

The mode as well as the duration of the transport hardly offers carrying capacities for small mammals in the Baltic Sea. Either it would last much too long or it would depend on extreme events such as floods and storms with very rough sea. Consequently, the probability of a hazel dormouse rafting on driftwood remains a rather theoretical thought.

Vegetation development in the Early Holocene – a prerequisite for the hazel dormouse spreading

According to recent investigations in north-eastern Germany (Theuerkauf et al. 2014), the warming at the Younger Dryas Holocene transition (about 11600 cal. yr BP) triggered the rearrangement of the vegetation across Europe. Birches, *Betula* spp., and

pine, *Pinus sylvestris*, formed the primal woodlands already 200-400 years after the first initials as largely separated stands of pines on well drained sandy and birches on fertile morainic soils. The hazel, *Corylus avellana*, started to spread at about 11200 cal. yr BP, yet the final expansion was delayed until about 10800 cal. yr BP. Subsequently the hazel established itself on fertile soils from which it rapidly expelled the birch to a large extent (Theuerkauf et al. 2014). Hazel pollen has been proven to constantly dominate many samples (Jahns et al. 2013). Probably, low summer temperatures delayed the expansion of more thermophilous tree taxa like elm, *Ulmus glabra*, lime tree, *Tilia cordata*, or oak, *Quercus robur* in Central Europe. These species only expanded at about 10000 cal. yr BP (Theuerkauf et al. 2014).

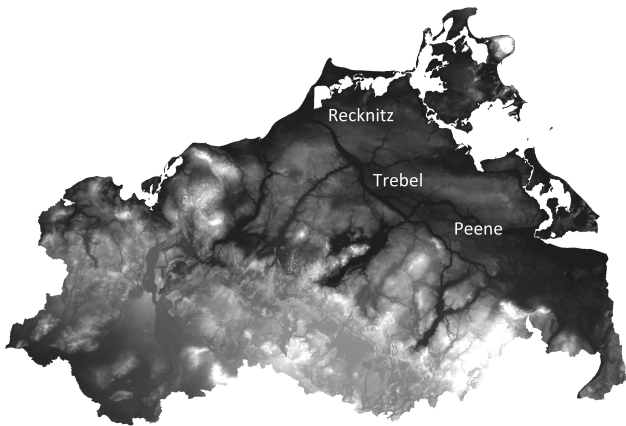


Fig. 3. Digital terrain model of Mecklenburg-Vorpommern, dark colours indicate valleys and lowlands (© GeoBasis-DE/M-V 2011).

Coherent hazel dominated woodlands could provide optimal habitats for the hazel dormouse allowing a recolonisation of the landscape after the glaciations. Palaeontological studies show hazel dormouse immigration in its modern peri-Baltic range in the Early Holocene (Aaris-Sørensen 2009, Fahlke 2009). Therefore, a general northward directed spread all over Europe nearly simultaneously with the hazel can be accepted. In the subsequent Atlantic period the climatic conditions improved (so-called post-glacial climatic optimum) and mean annual temperatures were higher than today. Ash, *Fraxinus excelsior*, appeared in the region while beech, *Fagus sylvatica*, and hornbeam, *Carpinus betulus*, followed several thousand years later (Jahns et al. 2013). However, the habitat conditions for the already established hazel dormouse did not deteriorate due to the change from hazel woodlands to high forest.

Potential barriers for hazel dormouse immigration into the Mecklenburg-Vorpommern mainland areas south-west of Ruegen

As has been shown, the immigration of hazel dormice from central to northern Europe was facilitated by the spread of hazel in the Boreal period. But hazel did not enter the pine dominated forests on well drained sandy soils (Theuerkauf et al. 2014). Sandy soils originate from glaciofluvial and glaciolacustrine deposits that are wide-spread in north-eastern Germany. Glaciofluvial sandur sediments deposited by proglacial melt water occur as wide belts in front of the ice marginal zones of the Weichselian glaciation (Katzung & Müller 2004). They are common in Mecklenburg-Vorpommern (Fig. 2), in Brandenburg as well as in Poland. Besides, there are large glaciolacustrine sand

basins in the Oder mouth area and in the coastal region east of the city Rostock. Probably the requirements for hazel dormouse immigration have never been ideal in these areas. Fossil hazel dormouse remains have been found at the palaeontological excavation site Pisede in central Mecklenburg dated 8000 yr BP (Fahlke 2009). So there is evidence that at least a few animals have passed some of the several “low comfort zones” of the sandur belts. But these populations did not survive. There are no fossil or contemporary hazel dormouse occurrences north-east of the sandur belt except the Ruegen dormouse population.

Beside the sandy landscapes, wide river valleys of the Peene, Trebel and Recknitz were additional and more serious barriers for hazel dormice on the way to Ruegen. These river valleys situated in East Mecklenburg and West Pomerania (Fig. 3) do not belong to the common type of glacial valley formed in front of a stationary inland ice sheet. The evolution of these valleys is connected with the final decay of the inland ice. Temporarily there was an ice dammed Lake (“Haffstausee”) which is to be found in the area of the modern river mouth of the River Oder that drained northwestwards. Its runoff formed the valleys of these rivers. Wide riverbeds with various channels and small lakes were formed by the drainage. The main configuration already was finished in the Younger Dryas period (Janke 2002). The younger landscape evolution modified the relief insignificantly. The Atlantic period represents the climate optimum of the Holocene that was characterized by fast rising ground and surface water tables. It was then that the appearance of the contemporary river valleys was formed. The runoff and the river width increased, meander and oxbow-lake evolution took place. Shallow water areas silted up very fast and a spacious mire development took place. Hazel dormice crossing these valleys seem very unlikely because of two barriers: the watercourse of the river itself and the extended wet peat bogs nearby which were covered with reed beds. The huge gap in the current range of the hazel dormouse in north-eastern Germany can be explained by that. Furthermore, it can be suggested that the immigration of the hazel dormouse to Ruegen did not emanate directly from the south.

The River Oder is the main river of Pomerania. Its catchment area comprises large parts of Poland and north-eastern Germany. Depending on the water level of the Baltic Basin, the position of the Oder mouth varied in the past. According to the level rise after the Pleistocene deglaciation it was translocated from the Bornholm Basin between Scania (Skåne) and Bornholm to the Arkona Basin between Ruegen



Fig. 4. The possible land sea configuration in the south-western Baltic ca. 10000 cal. yr BP, just prior to the onset of the transition from the Lake Ancylus to the initial Littorina Sea (Source: Björck et al. 2008, modified). Neither was there a permanently flowing water body in the Great Belt nor between the Iles of Møn and Falster in the Northwest and Ruegen Island and the Darss Peninsula in the Southeast.

and Bornholm to its contemporary position in the Oderhaff estuary (Kolp 1983, Hoffmann 2002). For example, according to nautical charts the drowned old Oder valley is situated east of Ruegen at about 25 m below sea level. The River Oder can be said to have formed a hazel dormouse immigration barrier giving a good explanation why the hazel dormouse is absent on Bornholm.

The islands of Öland, Gotland, Saaremaa and Hiiumaa also lack hazel dormice. These islands belong to the central Scandinavian area of glacio-isostatic rebound that has been taking place since the deglaciation. Because of the uplifting, original shoals become islands that have never been connected to the mainland (Björck 1995, Ekman 1996, Lemke 2005). Therefore hazel dormouse immigration could not have taken place via land bridges.

Palaeogeographical development of the south-eastern Baltic – drowned land bridges?

In the Early Holocene the palaeogeographical development of the south-western Baltic area

was determined by a regression of the freshwater Lake Ancylus followed by the marine Littorina Transgression. During these periods a formation of temporary land bridges connecting Jutland (Jylland) with Scania and north-eastern Germany appear to have been likely. The water covered areas subsided and became restricted to the deepest parts of the Mecklenburg Bay and the Arkona Basin as well as to smaller depressions (Lemke 1998, 2005).

The hypothetical River Dana was introduced to the scientific discussion to explain the Lake Ancylus regression via Darss Sill, Fehman Belt (Femern Bælt) and Great Belt (Storebælt) into Kattegat (von Post 1929, Kolp 1986, Björck 1995). The River Dana is supposed to have functioned from about 10300 to 8900 cal. yr BP (Björck 1995), but studies in threshold areas have failed to confirm its existence (Lemke et al. 1999, 2001). Therefore, the existence of a permanent hazel dormouse immigration barrier caused by an extensive fluvial system is not very likely.

The highest level of the Lake Ancylus between ca. 10400 and 10300 cal. yr BP was followed by a regressive development (Kolp 1986, Björck 1995, Bennike et al. 1998, Lemke 1998, Bennike et al. 2000, Jensen et al. 2005). At 9800 cal. yr BP the Lake Ancylus was lowered at least to the level given by the deepest thresholds at about 24 (22) m below sea level in the Great Belt and the Darss Sill, respectively (Lemke 1998). At this time the Darss Sill which is located between the German Darss peninsula and the Danish island Falster probably became dry land temporarily (Fig. 4). An environmental change is indicated by sedimentation in local lakes, bogs and swamps between about 9500 and 8800 cal. yr BP (Bennike et al. 1998, Lemke et al. 2002). A similar situation can be reconstructed for the Great Belt area. The late glacial sediments are truncated by an erosional unconformity overlain by Early Holocene freshwater sediments that include riverine, lakeshore and extensive lake deposits formed between about 10900 and 8800 cal. yr BP (Bennike et al. 2004). The deposition of the early river sediments is coeval with the maximum level of the Lake Ancylus.

The regression of the Lake Ancylus was followed by the marine Littorina Transgression. The initial sign of the marine ingress into the central Great Belt area is dated to 8100 cal. yr BP by marine shells (Bennike et al. 2004). Marine waters began to enter the Mecklenburg Bay 8000 cal. yr BP. In the Arkona Basin, the first marine signals are recorded approximately 800 years later, 7200 cal. yr BP (Rössler et al. 2011). The delay indicates that the Darss Sill did not have a spillway

for a certain period of time. The Darss Sill area, with a current threshold depth of about 24 (22) m below sea level, apparently has formed a barrier for incoming waters (e.g. Lemke 1998, Witkowski et al. 2005). That implies that the Darss Sill could be considered as a land bridge between Denmark and Ruegen at least for several centuries from about 9800 to 8800 cal. yr BP. Because Öresund (Øresund) was contemporaneously not yet flooded, a connection to the Swedish mainland seemed also be possible (Fig. 4).

Conclusion for the immigration of the hazel dormouse to the islands in the Baltic Sea

The palaeogeographic conditions clearly suggest that a coherent hazel dormouse population might have existed between Denmark, southern Sweden and north-eastern Germany until the modern Baltic Sea developed through the ingression of marine water. Hazel dominated woodlands and later mixed broadleaved woodlands are supposed to have been very suitable for the hazel dormouse.

Very few individuals of the hazel dormouse remain near their natal sites. Dispersal after independency is a characteristic of their life. Dispersing hazel dormice are able to travel very long distances in the forests, more than 3 km have already been documented (Juškaitis & Büchner 2013). According to Juškaitis (2014) early born juveniles settle their home ranges in a mean distance of about 360 m away from their natal site. Theoretically, the hazel dormouse could spread in wooded areas 20 to 40 km per 100 years. The distance of Ruegen to the nearest Danish island Møn is about 50 km and both

islands have been part of one mainland for at least 800 years before they became islands.

A microsatellite genotyping of hazel dormice in the south-west Baltic Region supports the geological interpretation. Mouton (in preparation) investigated hazel dormice from north-western Germany (n = 40), the Danish island Funen (n = 10) and the island Ruegen (n = 3). The samples could be clustered into four distinct genetic groups corresponding roughly to the geographic distribution. Hereby the individuals from Funen and Ruegen belong to one cluster, clearly genetically distinct from those situated in the German mainland (Alice Mouton, unpublished data).

Geographic implications of the possible migration route of the hazel dormouse

There has been a long debate among geologists, summarized by Björck et al. (2008), whether the land bridge between Denmark and Mecklenburg-Vorpommern was continuous and not interrupted by rivers or shallow waters. The hazel dormouse is rather reluctant to cross the open countryside and it is vulnerable to habitat fragmentation because of its arboreal way of life (Bright & Morris 1996). Assuming that the most probable migration route was directed from Denmark to Ruegen the Darss Sill has to be considered as dry land covered with forests.

Other animals could also have taken advantage of this way. Reconstructing possible migration routes and deeper insights in the genetics of animals could be therefore helpful in a better understanding of the landscape history in the Baltics.

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