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A new look at the dynamic western distribution border of *Apodemus agrarius* in Central Europe (Rodentia: Muridae)

Nový pohled na dynamiku západního okraje rozšíření myšice temnopásé (*Apodemus agrarius*) ve střední Evropě (Rodentia: Muridae)

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Abstract. During its postglacial westward expansion, *Apodemus agrarius* reached Austria in 1996 and until 2013 it colonised an area almost 140 km in length and 56 km in width in this country. Simultaneously, major range expansions were observed in Slovenia, Hungary, Slovakia and Moravia. Oscillations of the western distribution border in Central Europe during the 20th and 21st centuries coincide remarkably well with changes in mean summer and winter temperatures.

Key words. Range expansion, dynamic border, temperature change.

INTRODUCTION

Probably due to the Holocene warming between 9000 BP and 6000 BP (Preboreal to Older Atlantic), the range of *Apodemus agrarius* (Pallas, 1771) expanded rapidly from the centre of origin near the border of the Pacific Ocean (probably Far East Russia – Suzuki et al. 2008) to the border of the Atlantic Ocean (Kratochvíl & Rosický 1954 and many later authors). As a consequence of climatic deterioration during the Subboreal at ca. 2000 BP (Pavlenko 1998), the formerly continuous range became disconnected in Eastern Siberia between 105° and 120° E (Corbet 1978) due to desiccation. The young age of this transcontinental dispersal is corroborated by high similarity of genetic traits of the Far Eastern and Siberian-European populations (Atopkin 2007, Suzuki et al. 2008, Koh et al. 2014) and findings in Holocene deposits in Moldavia, Trans-Ural plain (cf. Atopkin 2007) and south-western Slovenia. Here, skeletal remains were found in prehistoric excavations dated to 9600–7800 BP and 7800–6000 BP (Toškan & Kryštufek 2006). As already demonstrated by Böhme & Reichstein (1966), the immigration of the striped field mouse to the Danish islands of Lolland and Falster (where it occurs until today – Hansen & Jensen 2007) proves that it arrived in north-western Europe before ca. 7200 BP when the transgression of the Litorina Sea had turned southern Scandinavia into a group of islands and peninsulas (Aaris-Sørensen 1992).

There are, however, indications that similar waves of range expansions had occurred already earlier, during the Pleistocene. In south-western France (Quercy, 44° 16’ N, 01° 43’ E), teeth

of *Apodemus* cf. *agrarius* were found in deposits that were radiocarbon–dated and calibrated to a glaciation interval between 17,417–17,044 BP, i.e. the end of the Younger Würm glaciation (Aguilar et al. 2008). The striped field mouse has also been reported from several considerably older Pleistocene levels in Europe (Kowalski 2001, Aguilar et al. 2008 and Janossy 1962, 1986); however, their taxonomic allocation was disputed controversially (e.g. Bauer 2002, Aguilar et al. 2008).

The western European distribution of *A. agrarius* exhibits a southern and a northern branch, both extending westward to 8–10° E longitude (Mitchell-Jones et al. 1999) (Fig. 2). Originating from Russia, the northern branch reaches the eastern border of the Baltic Sea, passes along its southern border and stretches to the Atlantic Ocean. The southern branch extends south of the areas that were glaciated or permafrost during the last Ice Age. It stretches from the northern (Ukraine) and western (European Turkey) border of the Black Sea south of the Carpathians and Alps across the Balkans and Istria to Italy north of the Po river (Friuli-Venezia Giulia westwards to eastern Piemonte – Capizzi & Filippucci 2008). Populations occurring in Istria and Italy are separated from those inhabiting the lowlands along the Sava and Mura rivers (Kryštufek 1985). This southern branch is probably the oldest part of the European range (Kratochvíl 1977). From here, *A. agrarius* colonised the large Carpathian basin, forming the central part of the European distribution. At the end of the 20th century, the western limit of this central range extended to about 20° E longitude (Mitchell-Jones et al. 1999).

During the 19th and early 20th century, the western distribution border of *A. agrarius* ran along Syddanmark (Denmark – Baagøe & Jensen 2007), Schleswig-Holstein (Böhme & Reichstein 1966), coastal areas between the Elbe and Weser rivers in Lower Saxony (Niethammer 1976) and the Rhine river (Blasius 1857) in Germany. However, by the 1960s and 1970s, the western limit had retreated to the southeast (Böhme & Reichstein 1966, von Lehmann 1976, Niethammer 1976, Kraft 2008). Currently, the north-western part of the range reaches, along the northern

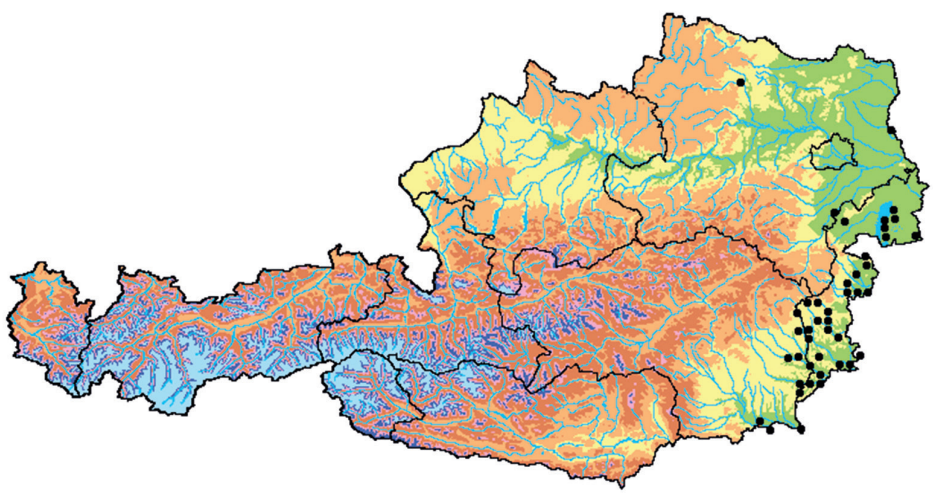

Fig. 1. Current (1996–2013) distribution of *Apodemus agrarius* in Austria.
Obr. 1. Současné rozšíření (1996–2013) myšice temnopáse (*Apodemus agrarius*) v Rakousku.

side of the Elbe river, the Eiderstedt peninsula (Schleswig-Holstein), with an isolated area of occurrence between the Elbe and Weser rivers (Elbe-Weser triangle, Lower Saxony). Further south the range is delineated in the west by the Weser river (from Nienburg, 52° 36' N, 09° 21' E to Göttingen, 51° 32' N, 09° 54' E) (Seebass 2001, Borkenhagen 2011). From the Danish mainland (Jutland) and northern Schleswig-Holstein, *A. agrarius* has disappeared (Baagøe & Jensen 2007, Borkenhagen 2011).

Large parts of the range were abandoned also in the Czech Republic (Bryja & Řehák 2002) or fragmented into isolated parts in Hungary (Schmidt & Topál 1976). More recently, however, indications of expansions in Central Europe have been published.

The aim of this paper is to describe the recent expansion of the central part of the range of the striped field mouse in Austria in relation to range extensions in other parts of Central Europe and discuss possible mechanisms underlying the Holocene transcontinental range expansion and the dynamics of the western border of the distribution area.

RESULTS

Six field mice trapped in southern Styria (Sicheldorf, Radkersburg) near the Slovenian border in 1996 constituted the first unambiguous record of *A. agrarius* in Austria (Spitzenberger 1997). In 2003, a dead field mouse was found in the reedbeds of Lake Neusiedl near Illmitz/Burgenland, some 135 km north of the first finding. Extensive trapping in the drained fen at Hanság near Andau at the Austro-Hungarian border yielded another two specimens in the same year (Herzig-Straschil et al. 2004). As a result of public relation work in newspapers and television in Burgenland and Styria, local people sent dead field mice and photographs taken with their mobile phones to the Natural History Museums in Graz and Vienna. These records filled the gap between the first and the second Austrian localities in the two provinces (Sackl et al. 2007) and markedly extended the known distribution area. Besides this main part of the Austrian distribution, there are two records from the lowlands north of the Danube in Lower Austria. Lauermann et al. (2011) reported that one field mouse was photographed in May 2008 when it was moving between bushes in grasses and weeds on the bank of the Kamp river near Rosenburg, approximately 30 km south of the Czech border. In April 2008, one *A. agrarius* was trapped in the floodplain forests of the March/Morava river near Zwerndorf, municipality of Weiden an der March. This river forms the border between Austria and Slovakia. Probably because of the mid-dorsal narrow dark stripe typical for *A. agrarius*, but resembling the colouration pattern of the northern birch mouse, this specimen was listed erroneously as *Sicista betulina* in the final report (unpubl.) of a project carried out by the Research Institute of Wildlife Ecology of the University of Veterinary Medicine in Vienna. The Austrian distribution of *S. betulina*, however, is confined to the Alps and the Bohemian Central Mountains (Spitzenberger 2002).

By 2013, altogether 76 verified records became known (Fig. 1). The current western distribution limit is situated at ca. 15° 30' E longitude. Without regarding the single localities in Lower Austria, the area colonised by *A. agrarius* between 1996 and 2013 covers a belt along the Slovenian and Hungarian border, reaching ca. 56 km in width and almost 140 km in length. The range occupies the eastern rims of the ecoregions of the Illyrian hills and terraces in the south and Pannonian lowlands in the north; the altitude of the localities varies between 115 and 400 m a. s. l. The species has now reached the south-eastern border of the Alps (Fig. 1).

The extension of the western limit of the European range of *A. agrarius* into Austria was a result of major range expansions in the countries neighbouring Austria such as Slovenia,

Hungary, Slovakia and the Czech Republic. Fig. 2 illustrates the extent of the expansion of the central part of European distribution since 1999 (Mitchell-Jones et al. 1999) in Austria and neighbouring countries.

There is no documented evidence of a former (before 1996) occurrence of *A. agrarius* in the Austrian territory, but two old mentions for Lower Austria published by Fitzinger (1832:

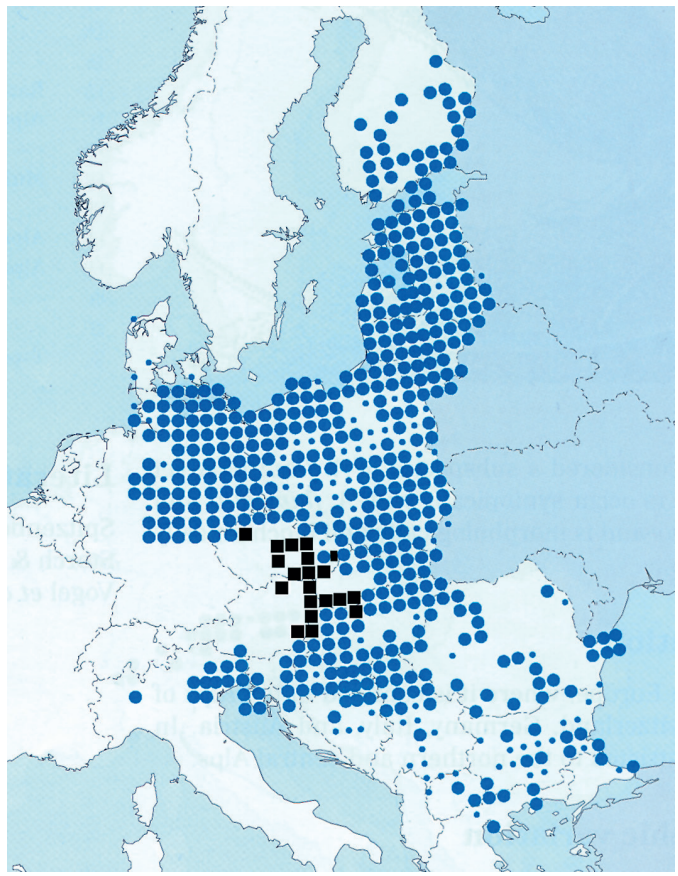

Fig. 2. UTM grid (50×50 km) map of the European distribution of *Apodemus agrarius*. Circles: distribution by 1999 (after Mitchell-Jones et al. 1999), squares: current distribution in Austria and neighbouring countries (Hungary, Slovakia and Czech Republic) as drawn from the following references: Ambros et al. (2010, 2012, 2013), Anděra (2011), Bryja & Řehák (2002), Flousek et. al. (2004), Heroldová et al. (2013), Kašpar & Anděra (2011), Polechová & Graciasová (2000) and Uhrin & Benda (2000).
Obr. 2. Kvadrátová mapa systému UTM (50×50 km) evropského rozšíření myšice temnopásé (*Apodemus agrarius*). Kroužky: rozšíření k roku 1999 (podle Mitchella-Jonese et al. 1999), čtverce: současné rozšíření v Rakousku a okolních státech (Maďarsko, Slovensko, Česko) na základě pozdějších zdrojů (Ambros et al. 2010, 2012, 2013, Anděra 2011, Bryja & Řehák 2002, Flousek et. al. 2004, Heroldová et al. 2013, Kašpar & Anděra 2011, Polechová & Graciasová 2000, Uhrin & Benda 2000).

"An der Gränze von Baiern, Böhmen und Mähren [at the [Lower Austrian] borders of Bavaria, Bohemia, and Moravia]"; repeated by Rothe 1875 and Mojsisovics 1897) and by Wichmann (1954: "Brunner Steinfeld") which were refused by Bauer (1960) as identification errors, could now be regarded as possibly valid.

Slovenia. In the valley of the Mur/Mura river, *A. agrarius* expanded over a distance of 12 km from Bunčani (north-westernmost record in 1985 – Kryštufek 1985) in Slovenia to Sicheldorf in Styria (locality of the first Austrian record in 1996) in the course of 11 years at maximum (1985–1996).

Hungary. Although detailed evidence is missing, it can be assumed that the immigration to Burgenland originated from Hungary. Until the middle of the 20th century, the field mouse was widespread in Hungary (Schmidt & Topál 1976). Solymosy (1939) reported a record from Nagylósz, 6 km east of the Austrian border which was considered as misidentification and hence refused by Bauer (1960) and also by Schmidt & Topál (1976). However, the latter authors retained a record from Türje, 45 km east of the Austrian border, as a valid occurrence for the mapping period until 1945. After 1945, the Hungarian range of *A. agrarius* became strongly contracted and was divided into two main parts, one northeast of the Great Pannonian Basin and the other one southwest of Transdanubia with the northernmost locality at Lake Balaton (Schmidt & Topál 1976). A small third distribution island was located at the Danube, up- and downstream of Budapest. By 2007, *A. agrarius* occurred again in all parts of Hungary (Bihari 2007). The most likely source of the westward expansion into Austria are the Hungarian populations between the rivers of Zala and Rába/Raab and Répce/Rabnitz and Rába/Raab (Bihari 2007); the closest record from the latter area (Csorna – Gubányi et al. 2002) lies just about 15 km southeast of the Austrian border.

Slovakia. Ambros et al. (2010, 2012, 2013) investigated the north-westward spread of *A. agrarius* along the Danube river in Slovakia. In 2010, Ambros et al. (2010) reported the discovery of a new occurrence of the striped field mouse in lowlands along the northern bank of the Danube river between Bratislava and Komárno, possibly an offspring of the small isolate near Budapest known for a long time (Schmidt & Topál 1976). Two years later, Ambros (2012) found this species in Svätý Jur (47° 58' N, 17° 38' E), 15 km north-north-west of Bratislava and 29 km south-east of Zwerndorf upon March/Morava (48° 30' N, 16° 50' E) in Austria.

Moravia. The Austrian record made in 2008 in Rosenburg (Lauermann et al. 2011), lying 29 km from the Czech border, can be regarded as a part of the rapid expansion of the field mouse in southern Moravia, Czech Republic. From here, Polechová & Graciasová (2000), Bryja & Řehák (2002) and Heroldová et al. (2013) reported many new records of *A. agrarius* from the districts of Olomouc, Znojmo, Brno-město, Prostějov, Zlín, and Kroměříž. Some southernmost Moravian records lie less than 10 km from the Austrian border. These findings probably validate the records collected between 1920 and 1940 by Farský (1965) which had been put in doubt e.g. by Kratochvíl (1976).

DISCUSSION

To understand the mechanisms underlying the conspicuous transcontinental range expansion of *A. agrarius* and the oscillations of the western border, its ecology and reproductive output should be regarded. In general, the striped field mouse occupies an exceptionally broad ecological niche. The only factors limiting its occurrence are the dependence on moist components

in the food and absence of dense forests (Karaseva et al. 1992). According to these authors, *A. agrarius* reaches the highest population density in Far East Russia in the zone of broadleaved evergreen forests which are nowadays largely turned into farmland; here it is the most abundant and dominant rodent, more or less equally distributed over all habitats; seasonal and annual

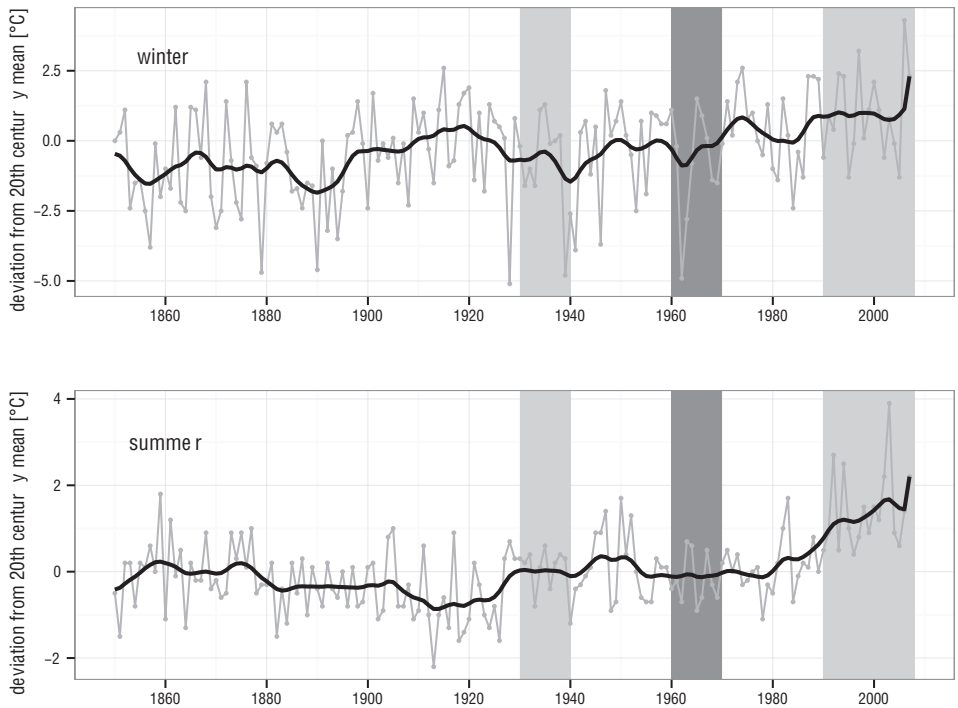

Fig. 3. Annual mean summer (June to August) and winter (December to February) temperatures in the North-eastern Alpine sub-region (eastern Austria, eastern Slovenia, southern Czech Republic, western Slovakia, and western Hungary; sub-region centre at 47° 40.8' N, 15° 00.5' E) between 1850 and 2007. Approximate periods of extended western distribution border of *Apodemus agrarius* are shaded light grey, periods of contracted western distribution border are shaded dark grey. Mean annual temperature records are shown as solid grey lines, solid black lines are underlying trends obtained by a Butterworth low-pass filter. Data are taken from the 'Coarse Resolution Subregional Means' dataset in the HISTALP database (Auer et al. 2007).

Obr. 3. Průměrné letní (červen až srpen, dole) a zimní (prosinec až únor, nahoře) teploty v severovýchodní alpinské podoblasti (východní Rakousko, východní Slovinsko, jižní Česko, západní Slovensko a západní Maďarsko; střed podoblasti je na souřadnicích 47° 40,8' N, 15° 00.5' E) mezi lety 1850 a 2007. Přibližná období posunu hranice rozšíření myšice temnopásé (*Apodemus agrarius*) na západ jsou zabarvena světle šedě, období stahování areálu na východ jsou zabarvena tmavě šedě. Průměrné roční teploty jsou vyznačeny nepřerušovanými šedými čárami; černou čarou jsou propojeny hodnoty Butterworth low-pass filter. Údaje jsou převzaty z database HISTALP, souboru 'Coarse Resolution Subregional Means' (Auer et al. 2007).

fluctuations in numbers are very small. In the foothills of the Altai, Caucasus, Carpathians Mts. and in the Volga delta, it inhabits humid parts of cultivated areas; here the abundance is somewhat reduced and the population numbers are relatively stable. In the zone of former forest steppes from Krasnojarsk (west of Lake Baikal) to western Ukraine, the striped field mouse is largely synanthropic; it is abundant only in optimal habitats like marshy floodplains and arable fields; seasonal and annual fluctuations in numbers can be high. In European Russia, *A. agrarius* is highly dependent on man-made habitats and exhibits huge annual fluctuations in numbers including deep and continued depressions in reproductive success. In central Europe, besides human buildings and urban habitats such as parks, it uses all kinds of fields, permanent grassland, littoral vegetation and reeds, corn ricks and open woodland, but also interzonal and badly disturbed, waste habitats (Zejda 1967). In addition, *A. agrarius* is omnivorous (insects and their larvae, spiders, molluscs, annelids and vertebrates such as frogs and small mammals, carrion, seeds, cereal grains, fruits and green parts of plants, e. g. Holišová 1967, Böhme 1978). Seasonal food habits shift as food availability changes.

The gradual deterioration of the animal's environment and its reproductive output from east to west (Karaseva et al. 1992) seems to be affected by a gradual change of climate. The current vast distribution range of *A. agrarius* lies in an interrupted Eurasian belt of rainy climates. They vary from east to west from rainy with severe and dry winters and highest summer temperatures above 22 °C in the Russian Far East to rainy with mild winters, lack of a dry period in winter, and highest summer temperatures below 22 °C in Europe (Times Books of London 2011).

The reproductive output of the striped field mouse can be very high under optimal conditions. The litter size is the largest among the European *Apodemus* species (maximum 8 – Stein 1955, average 6.64 – Pelikán 1965). In the climate of Shanghai (similar to that of the Russian Far East), the mouse exhibits two breeding peaks (in spring and autumn) and a breeding interruption in winter of only 3–4 months (Zhu & Qian 1982). The latter authors also showed that in the Shanghai population, the numbers of embryos as well as the numbers of specimens surviving the winter were higher in warmer years than in colder years. In the climate of western Europe, however, the duration of the breeding interruption is six months and the peak of subadult individuals occurs only once, in autumn (Pelikán 1965). Nevertheless, in favourable years and favourable habitats the striped field mouse can produce large numbers of offspring which will spread into suboptimal or even pessimal areas, thus producing local outbreaks and leading to range expansions.

Indications of an extended range of *A. agrarius* (Solymosy 1939, Farský 1965) between 1930 and 1940 fall into a period of moderate summer and winter temperatures (Fig. 3). After this period, several exceptionally cold winters followed (1939–1941, 1946, 1960–1961) which might explain the rapid loss of large parts of the central and western European range during this period. The period of the current expansion in the central European range is characterised by a steep and still ongoing rise in summer temperatures since the 1980s. The invariably relatively warm winters during this timespan may have enhanced the rapid spreading.

Our results seem to confirm the influence of climate, in particular temperatures on the range expansion and oscillating western distribution border of *A. agrarius*. The high fecundity of this species, its ecological plasticity and the readiness to adjust to conditions of urban environments, especially during winter (Volkov et al. 1979, Böhme 1978, Babinska-Werka et al. 1979, Zhu & Qian 1982), probably facilitated the transcontinental spreading. It seems likely that the postglacial westward expansion was triggered by the Holocene warming, that it started before dense forests covered the landscapes completely and was enhanced when Neolithic man opened

the forests for agriculture and human settlements. The ongoing fragmentation of forests and urbanisation of the landscape as well as the present climate change improve the conditions for establishing and spreading of populations in Central and Western Europe.

SOUHRN

V průběhu v poledové době probíhající expanse na západ dosáhla myšice temnopásá (*Apodemus agrarius*) hranic Rakouska a v letech 1996–2013 kolonisovala téměř 140 km široké a 56 km hluboké území této země. V téže době byly pozorovány expanse areálu také ve Slovinsku, v Maďarsku, na Slovensku a na Moravě. Tato středoevropská oscilace západní hranice areálu rozšíření se výrazně shoduje se změnami průměrné letní a zimní teploty během 20. a v 21. století.

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