The European beaver (Castor fiber) was a common species in the rivers of Europe and northern and eastern Asia until the late 19th century (Nolet & Rosell 1998; Halley & Rosell 2002, 2003; Halley et al. 2012). By the beginning of the 20th century, the global population had been reduced to eight isolated populations: in the Rhone Delta (France), on the middle Elbe (Germany), in south Norway (Telemark), in the Dnieper river system in Belarus and the Ukraine, in the Voronezh-Don-system (Russia), at the villages of Milhost (Miglécnéméti) and Buzica (Buzita), in Slovakia. According to our calculations, the present total beaver population in Hungary is between 4,000 and 5,000 and 14,600–18,300 beavers with potential support. For Slovakia, we estimated the potential population size to be 7,700–9,600. Our findings in northern Pannonian lowland (Slovakia–Hungary border) are an important evidence of beaver expansion. Although we don't know the exact origin of investigated population, these new records indicate the possibility of merging the populations of different origin, which could enable gene flow and increase the genetic diversity. This could lead to improved recovery of species and its stabilisation in nature. However, it is necessary to carry out a detailed investigation of the presence of beaver in these regions in future.

INTRODUCTION

The European beaver (Castor fiber) was a common species in the rivers of Europe and northern and eastern Asia until the late 19th century (Nolet & Rosell 1998; Halley & Rosell 2002, 2003; Halley et al. 2012). By the beginning of the 20th century, the global population had been reduced to eight isolated populations: in the Rhone Delta (France), on the middle Elbe (Germany), in south Norway (Telemark), in the Dnieper river system in Belarus and the Ukraine, in the Voronezh-Don-system (Russia), in the Konda and Sosva rivers (East Ural region, Russia), on the upper Yenisei and Azas rivers (Russia, Tuva Republic) and in the Bulgan river (Mongolia/China). Nevertheless, in recent decades, protection, natural spreading and reintroductions have resulted in a rapid recovery in the numbers and range of this species, particularly in continental Europe and, recently, also in Great Britain (Halley & Rosell 2002; Halley et al. 2012; Stringer & Gaywood 2016). Halley et al. (2012) have shown that the beaver is currently established in all countries within the species’ former natural range in continental Europe, with the exceptions of Portugal, Italy and the southern Balkans. The continuous population ranges from Germany through Poland, the Baltic States, Belarus and Ukraine to central Siberia in the Russian Federation. A second large disjunctive population and smaller scattered isolated populations through the rest of mainland Europe are located in Norway and Sweden. Isolated reintroduced populations have also been recorded in distinct locations outside the former Soviet Union, for example, in Poland (Dziciolowski & Gozdiewski 1999).

In Slovakia, beaver was exterminated during 19th century, mainly because of hunting for meat, fur and castoreum with the shot in 1858 at Žitný Ostrov. The species began to gradually spread again in 1977 from Austria and since 1981 from Poland (Valachovič 2012). The author summarised all published and unpublished data and estimated that the oc-
currence of beaver has been recorded in about 11.6% of the territory of Slovakia. This is very important because the beaver was absent from Slovakia for 150 years. Since 1977, the south-western population has grown dynamically in the catchments of the Morava and Danube rivers. In contrast, the beaver only appeared more recently in north-eastern Slovakia in 1981. Valachovič (2012) summarised several older findings from eastern Slovakia and showed the first occurrence on the Ondava river; then on the Poprad, Topľa, Dunajec and Cirocha rivers, and, finally, on the upper part of the Laborec river. All observations confirmed that the species predominantly inhabits lowlands in the region. Moreover, the beaver occupies about 30% of the potentially suitable parts of Slovak territory (about 56% of Slovakia’s entire territory), and restoration of the population runs in two phases (Valachovič 2012; Halley et al. 2012). The first phase includes rapid growth of newly colonised territories, up to the nearest barrier. The second phase, which began approximately in 1999, includes a rise in the population size, during which the beavers increase their population by also colonising suboptimal localities. In this phase, the population size has started to grow exponentially.

The history of extinction and re-settlement was observed in Hungary as well. The distribution in Hungary shows that the beavers became extinct in 1865, mostly because of overhunting, and were absent from Hungarian fauna for 130 years. They appeared again in the Szigetköz area (Bajomi 2011a, b). Similarly, several authors (Boszér 2001; Bera 2007; Bera & Gruber 2007; Bajomi 2011a, b; Bajomi et al. 2016) showed that these animals probably wandered here from a population successfully established by reintroduction in Austria. In 1988, beavers were also found near Lake Tisza. This small population was later augmented with seven more animals by the staff of the Hortobágy National Park Directorate. Later, authorities realised that the reintroduced specimens were actually Canadian beavers (Castor canadensis). For this reason, the last living animals (some had already died) were trapped by park rangers. Moreover, between 1996 and 2008, more than 200 beavers were reintroduced in the areas of Gemenc and Hanság and in area next to the Tisza and Dráva rivers. Most of these beavers came from Bavaria and Germany, and some animals from Austria.

In the present study, we provide the first knowledge of the occurrence of the species in south-eastern Slovakia, on the Slovakia–Hungary state border. We discuss whether these occurrences at the state border represent the beginning of the spread with potential gene flow, for example, mixing of two populations between Hungary and Slovakia.

1. MATERIAL AND METHODS

The first presence of the beaver was confirmed in the vicinity of Slovakia–Hungary state border, at the village Milhôst (Miłećnemetsi in Hungarian), 48°31’47.3"N, 21°17’15.8"E, 156 m a.s.l. (Figs. 1a, 1b, 2). Therefore, further distribution research was carried out by the method of direct searching for the presence of signs, mainly damaged trees, dams, signs of food consumption (chewed/felled trees), footprints in the mud, and so on along the Tornyša and Hornád (Hernád in Hungarian) rivers and its tributaries in the period from 6 June to 20 July 2016. The research was done by walking next to the water. First, the southern part of the Košická kotlina basin, away from the city of Košice in the direction of the Hungarian border, was examined. In addition to the direct search, we also had conversations with local residents. Overall, 18 municipalities and their surroundings were checked (Belža, Čaňa, Geča, Kokšov-Bakša, Nižná Myšľa, Krásna nad Hornádom, Bohdanovce, Košická Polianka, Sady nad Torny, Olšovany, Nižná Hutka, Vyšná Hutka, Zdaňa, Trstené pri Hornáde, Perín-Chym, Buzica, Komárovce and Veľká Idá). We also checked the surroundings of watercourses in nine Hungarian villages (Abaujvár, Telkibánya, Bózsa, Pálháza, Mikóháza, Tornyosnémeti, Hidasnémeti, Hernádzsurdok and Zsuja).

In addition to direct searches for the beaver presence signs, we tried to determine the number of individuals by the number of bitten or gnawed trees (Dyakov 1975). This method is based on the total number of completely (felled) and incompletely gnawed trees and their dimensions (diameter of the trunk) and then calculating the index which determine the approximate number of individuals. Finally, we have estimated potential total beaver population in Hungary and Slovakia from beaver families, that is, territories.

2. RESULTS AND DISCUSSION

From all the above-mentioned and controlled areas in Slovakia, only 22 damaged purple willow (Salix purpurea) trees from the autumn and winter seasons were found with completely gnawed trunks on the shore of a lake formed by a former gravel quarry near Milhôst (Figures 1a, b and 2). We used the method of Dyakov (1975) to estimate the population size of beaver and confirmed the presence of approximately 3 individuals, which is consistent with the presence of one family (Table 1). Moreover, gnawed trees, including five gnawed willows (all were 16.0 cm in diameter), were also found at the confluence of two streams, Szartos-patak stream and Sokoliansky potok stream (Figure 1b). This record is very important because it is probably the gateway to the water surface of the lake or forms a new migration route northwards or southwards. The damaged trees were not only from the autumn and winter seasons, but we also found freshly gnawed willow branches, which is the evidence for the survival of beavers in the studied area. These observations are significant because according to the local fishermen, the first occurrence was observed approximately two years ago. Nevertheless, it should also be noted that the beaver was first observed already on 3 March 2016 in the vicinity of Buzica village (Buzita in Hungarian), at the confluence of Ida river and Perinsky kanál channel (48°32’49.9”N, 21°05’26.6”E, 189 m a.s.l.) by the last of co-author of this paper. Therefore, this data was checked again on 20 July 2016 and the beaver presence was confirmed again at this new site by finding a dam and four freshly damaged trees of alder (Alnus sp., 2.0–6.0 cm...
in diameter, i.e. one individual, Table 1). Similarly, the occurrence on this site was older, might be from winter season 2015. All these findings represent the first knowledge of the occurrence in south-eastern Slovakia.

The total size of the surveyed area is about 5,570 km$^2$ (this is not the full area shown on Figure 2, but only the part where we have data about the beaver presence). We calculated an estimate of the number of beavers living in this area. Currently, in Central European countries, we count 4–5 individuals for one beaver family, that is, territory (G. Höltzer pers. comm.).

We know about 219 territories on the study area, so the population size is between 870 and 1,100 (Table 2, see Appendix 1). This is probably an underestimate, because we do not know all the territories. Population density in this area is between 0.16 and 0.20 individuals per square kilometres. According to our latest calculations, the present total beaver population in Hungary is somewhere between 4,000 and 5,000. The total area of Hungary is 93,030 km$^2$, so the country can potentially support 14,600–18,300 beavers. Population estimates for Slovakia (49,035 km$^2$) are 7,700–9,600.

Figure 1a. Distribution of European beaver in Slovakia modified after Valachovič (2012). Notes: big black solid circle represents permanent occurrence since 1965; small black solid circle represents temporary occurrence. The red solid circles show new records on south-eastern Slovakia with the possible routes of immigration. The open blue circle represents the possible occurrence along Bodrog river in Slovakia.

Figure 1b. Locations of European beaver (Castor fiber) observed in the south-eastern Slovakia: Milhost (Miglécnémeti in Hungarian) and Buzica (Buzita in Hungarian) villages (Source: ©2015 Google, Image©2015 CNES/Astrium)
First, this is very interesting in relation to migration between two countries, Slovakia and Hungary, with both mixing of population and gene flow. On the other hand, it is very important in relation to the ecosystem because the beavers transform new habitats and have negative and/or positive impact on other animals and the landscape.

As it was mentioned earlier, the first current finding of the species in north-eastern Slovakia was confirmed along the Ondava river in 1981 and it was expected that animals came from Poland (Valachovič 2012). On the other hand, the history and the current situation in Hungary were very comprehensively summarised by Bajomi (2001a). The last specimen in Hungary was hunted in February 1854 near Ács in Komárom-Esztergom county (Wachsmann 1905), and the last observation on the territory of current Hungary was made at the Danube river near Ács in February 1858 (Brehm 1929). In 1985–1986, after almost 130 years of absence from the Hungarian fauna, beavers appeared again in Szígetkőz area of the western country. Later, the Hungarian beaver reintroduction programme began in 1994. More than 90% of the beavers reintroduced in Hungary originated from Bavaria, from the Regensburg, Bavarian
Forest and Danube region (see Schwab & Schmidbauer 2003). The Bavarian population was established also as a result of a reintroduction programme between 1966 and 1980 and the animals came from Italy and Poland. The rest of the animals reintroduced in Hungary came from Austria and Poland. Since the reintroduction, Hungarian beaver populations have been monitored and it is showing a growing tendency (Figure 2).

After massive population bottlenecks and regional extinctions, beavers currently show a stunning comeback throughout Western and Central Europe (Halley et al. 2012). Therefore, this comeback is considered a major conservation success. Isolation of surviving populations in eight refugia (see Halley & Rosell 2003) caused this massive bottleneck reduced genetic diversity, led to inbreeding and reduced adaptive potential (Ducroz et al. 2005; Durka et al. 2005; Frosch et al. 2014). On the other side, as a result of the various reintroduction programmes in the 20th century, beavers from multiple source localities were released and they now form viable populations (Frosch et al. 2014). These programmes differed in their reintroduction strategies, that is, using pure subspecies vs. mixed source populations. Recently, Frosch et al. (2014) have shown via evaluation of mitochondrial and nuclear DNA markers that beavers of various populations in Central Europe (i.e. from Germany, Luxembourg, Belgium and Switzerland and all with different source populations co-occur in spatial vicinity, forming potential intraspecific hybrid zones) were well admixed, which form genetically diverse populations that spread across the study region. They also suggest that the merging of different lineages is already progressing in all studied regions. We assume that it is also important regarding our findings in northern Pannonian lowland (Slovakia–Hungary border). Regardless of the origin and genetic analysis of both the populations, their spreading is evident. Moreover, their meeting in the near future will lead to mutual genetic exchange and increased genetic diversity. In addition, as mentioned earlier, beavers in Slovakia and Hungary have different origins (not only via immigration from Poland and Austria but reintroduced populations had a different genetic background from source countries, e.g. Poland, Bavaria, Germany, Italy, Lithuania and Belarus). Based on these statements coupled with the previous genetic analyses (e.g. Ducroz et al. 2005; Durka et al. 2005; Frosch et al. 2014), we believe that merging of separated European populations will lead to a gradual recovery of species and its stabilisation in nature. Halley et al. (2012) assumed that if the current trends continue, beavers will be fairly common mammals in much of Europe. Range expansion through the watershed is rapid, but population expansion is relatively slow. The reason for this is that the animals select the best habitat available, rather than settling close to their natal territory. Nevertheless, several furthest distance colonisations were reported by Saveljev et al. (2002) and Fustec et al. (2001). Later, Halley et al. (2012) showed that in most countries of the western and central European mainland, beavers occur at relatively low numbers for the present, and there is much unused suitable habitat. They also presented distribution maps with probably conservative distribution of species; but, on the other hand, the authors also expected an expansion in populations and range in the coming decades, especially in Western Europe and the Danube watershed. Similarly, our own unpublished data on the distribution range shift in Slovakia along the Ondava, Topfa, Torsya and Laborec rivers are in accordance with the previous data obtained for the spread of the species after being introduced into new areas (Bozsér 2001; Halley & Rosell 2002, 2003; Bera 2007; Bajomi 2011a, b; Halley et al. 2012; Valachovič 2012; Vorel et al. 2012). According to the above-mentioned facts, we examined several different migration routes for our records at the state border. The first and second paths of migration were along the Hornád and the Ida rivers from Slovakia. Nevertheless, our own data throughout the southern part of the Košická kotlina basin show that the species is not present in this region (Figure 2). Insufficient information on the distribution does not mean that the species is not present in these areas, and in fact, the gap between the northern and southern localities may not be so great. Therefore, the distribution of species in Slovakia according to the map by Valachovič (see Figure 1a), it will be necessary to correct and update the current data on spread and expansion not only in the eastern part of the country.

Similarly, the route through Hungary along Hernád river is less likely, because it passes upstream along the river and because of the negative findings (see Figure 2). Nevertheless, we cannot completely exclude it because upstream movement was also confirmed by Saveljev et al. (2002). However, we did not confirm the presence of the species on the basis of habitation features in the surrounding villages along the Hernád river in Hungary (i.e. Tornyozsnémet, Hidasnémet, Hernádszurdok and Zsujta). Moreover, from Hungary distribution map, it is evident that there are long empty gaps along the Sajó and Hernád rivers without beaver territories. Nevertheless, there have been no systematic surveys in Hungary close to the border along the rivers. According to the Hungarian experiences, more beaver territories should exist along the upper part of Hernád river. During summer season, the beaver signs are almost unperceivable. The beaver’s migration in the river systems is much more common than that between the river systems; therefore, the most feasible migration route of the newly found beavers is the Hernád.

Another option would be intrusion along the tributaries of the Bodrog river. On the basis of the species distribution in Hungary (Figure 2), we assumed a possible way through the Bózsva stream westward. Our own observations and the information collected from the residents of surrounding villages (Abáujvár, Telkibánya, Bózsva, Pálháza and Mikóháza) were again negative. In addition, the finding in the vicinity of Buzica village indicates possible route along Ida river from Slovakia or Bodva (Bódv in Hungarian) river and its tributaries from Hungary. The records obtained by Saveljev et al. (2002) and Fustec et al. (2001) are very important for the interpretation of our negative findings in the other part of southern Slovakia and neighbouring Hungary. Moreover, the distribution of animals should reflect habitat suitability, with the assumption that food
resource directly influences home-range size. Regardless of where individuals recorded in south-eastern Slovakia come, in the future, there will be a need for detailed monitoring of their occurrence and further spreading.

The impact of beavers on landscape changes is very important (Kurstjens & Bekhuis 2003; Janiszewski et al. 2014). The engineering activities of beaver change the character of streams fundamentally by creating new habitats and increasing water retention (Żurowski 1992; Janiszewski et al. 2014). The effects of their foraging activities are mainly visible in fall and winter when the beavers cut down trees and shrubs in the vicinity of rivers and its tributaries. Animals monitor water levels in ponds continually, and any damage to dams is repaired immediately. Moreover, when water levels are high, beaver regulate them by releasing waters through relief canals. Several studies confirmed that beavers alter stream ecosystems by dam building resulting in a lower stream velocity, retention of sediments and organic matter as well as modifying physical, chemical and geomorphological conditions in these streams. Not only a significant impact on the fluvial processes and the environment (e.g. Balčiauskas & Ulevičius 1995; Ulevičius & Balčiauskas 1995, 1999; Cywicka & Brzuski 2008; Czech 2010; Kobojej 2013; Rurek 2013; Rurek et al. 2013; Święcicka et al. 2014; Giriát et al. 2016, Stringer & Gaywood 2016) but also a positive and/or negative effect on many plant species (Boczoń et al. 2009; Obidziński et al. 2011), invertebrates (Arndt & Domdei 2011) as well as vertebrates (Balčiauskas & Ulevičius 1995; Dalbeck et al. 2009; Kukuła & Bylak 2010; Ciechanowski et al. 2010, Manikowska-Ślepowrońska et al. 2016; Stählberg et al. 2017) was shown. Janiszewski et al. (2014) showed 19 types of activities that beavers played in ecosystems, which transform their natural habitats.

In conclusion, although we have not confirmed more appearance of beavers on both sides of the border, we believe that the tributaries of the Hornád and the Ida rivers are the most likely routes for the spreading of the beaver from Slovakia to Hungary. On the other hand, the Hernád and the Bóda river may represent a new migration routes from the opposite direction from Hungary. The distribution of species in Slovakia according to the data summarised by Valachovič (2012) is currently outdated; therefore, it will be necessary to correct and update the current data. We believe that it is necessary to carry out a detailed investigation of the occurrences in both sides of state border. Our findings in northern Pannonian lowland (Slovakia-Hungary border) were important for the evidence of beavers spreading. We don’t know their origin, that is, whether they came from Hungary or Slovakia; these new records indicate the possibility of meeting and mixing of populations with gene flow and increased genetic diversity. We believe that mutual mixing of individual European population will lead to a gradual recovery of species and its stabilisation in nature. Moreover, the return of the beaver in the wild not only in Slovakia but also in Europe has a positive/negative impact on the natural environment, fauna, flora as well come back of medium and large carnivores in Europe.

Acknowledgements: We thank anonymous referees for their valuable comments on the manuscript.

References


Bajomi, B. (2011b) Az eurázsiai hód (Castor fiber) visszatelepítésének tapasztalatai Magyarországon. 54 pp. (in Hungarian)


Wachsmann, F. (1905) Az utolsó hód Magyarországon. Állattani Közlemények, (4-5), 235–236. (in Hungarian)