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ORIGINAL PAPER

Muskrat (*Ondatra zibethicus*) decline after the expansion of American mink (*Neovison vison*) in Poland

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Abstract Field survey data in Central Poland revealed that the proportion of sites inhabited by muskrats decreased from 44% to 7% over one decade. This corresponded to the decline in hunting bags of muskrat over the whole of Poland. The largest hunting harvest of muskrat was recorded in 1987/1988 (66,416 individuals), the smallest in 2007/2008 (4,567 individuals). The decline in hunting bags occurred in all regions analysed; however, it was most rapid in the north and north-east. Before the expansion of mink, which started in northern Poland at the beginning of the 1980s, muskrat densities in particular regions depended on the availability of aquatic habitats. A comparison of hunting bags of muskrat and American mink in years 2002–2008 indicated a significant negative correlation between the numbers of these two species harvested in seven regions of Poland. The negative correlation between numbers of muskrat and mink suggests that mink predation is one of the most important factors in the decline of the muskrat population in Poland.

Keywords Invasive species · Population dynamics · Predation

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Introduction

Muskrats (*Ondatra zibethicus*) have been farmed in Europe since the beginning of the twentieth century, and their subsequent expansion has been studied in several countries (Artimo 1960; Becker 1972; Danell 1977; Nowak 1966). Muskrats spread naturally to Silesia region in Poland from the Czech Republic (Bohemia region) in the 1920s. Initially, the population expanded its range from south to north along large river valleys such as those of the Odra, Vistula and Warta (Nowak 1966). In the following years, the expansion from the south was supported by muskrats that had escaped from Polish fur farms located in different areas of the country. At the beginning of the 1940s, a stable muskrat population was present in southern Poland, and smaller isolated populations were also recorded in the central and northern parts of the country (mainly in the Vistula river valley). By the end of the 1950s, muskrats inhabited the whole country, and the population continued to increase during the early 1960s (Nowak 1966), i.e., about 40 years after first record of this species in Poland. However, in the second half of the 1980s, the first signs of a reduction in muskrat numbers in northern Poland were reported (Balerstet et al. 1990). Balerstet and co-workers suggested that this decline was related to the expansion of American mink (*Neovison vison*), and they anticipated further reduction in muskrat numbers. American mink began to colonise Poland at the beginning of the 1980s, and this process has been examined in several studies (Brzeziński and Marzec 2003; Romanowski et al. 1984; Ruprecht 1996; Ruprecht et al. 1983). In 2002, mink was declared an official game species, and since that time hunting bags have been recorded by the Polish Hunting Association.

The aim of this study was to examine muskrat population dynamics in different regions of Poland over the last 25 years in relation to changes in the population of its main predator: the American mink. Hunting bag records of muskrat and American mink for the whole of Poland were combined with the results of local field studies of both species and data on the regional availability of aquatic habitats.

Materials and methods

To compare the population dynamics of muskrat and American mink in various regions of Poland, hunting bag records from 49 hunting districts covering the entire country were obtained from the Polish Hunting Association. Recordings of the numbers of muskrat and mink taken began in 1981 and 2002, respectively. The data were pooled within seven large geographical regions of Poland (Fig. 1): north-east (NE), six districts, 52,500 km^2, basins of the lower Bug and Narew rivers, lakeland; north (N), five districts, 36,500 km^2, basin of the lower Vistula river, lakeland; north-west (NW), five districts, 43,300 km^2, basins of the lower Odra and lower Warta rivers, lakeland; south-east (SE), six districts, 35,900 km^2, basins of the middle Vistula, middle San and Bug rivers; central (C), ten districts, 48,900 km^2, basins of the middle Warta and middle Vistula rivers; south-west (SW): seven districts, 40,500 km^2, basin of the upper and middle Odra river, Sudety mountains; south (S), ten districts, 55,100 km^2, basins of the upper Vistula, upper Warta and upper San rivers, Carpathian mountains.

Field studies on muskrat distribution were conducted in years 1996–1998 and in 2006–2007. The study area was located in central Poland (Fig. 1), in the catchments of the middle Vistula, lower Bug and lower Narew rivers, and covered five hunting districts. The field survey was based on the recording of muskrat tracks and droppings along the banks of rivers, streams and ponds at 249 sites during both study periods. At each site, a distance of 200 m stretch of bank was searched for signs of muskrat habitation. If no signs of muskrat were found, the site was recorded as negative. Additionally, in years 2004–2007, American mink were captured in ten areas of Poland using live traps (Fig. 1). The total trapping effort of 1,008 trap nights resulted in the capture of 76 mink.

To estimate the impact of American mink on muskrat populations, we used Before–After Control-Impact (BACI) design analysis. On the basis of recent (2002/2003–2007/2008) hunting bags of mink (see "Results") and information from questionnaires sent to hunters (Brzeziński and Marzec 2003), Poland was divided into two areas according to the present abundance of mink. Regions with low mink densities (C, S, SE) were treated as a "Control" area in the BACI design, whereas those with high densities (N, NE, NW, SW) were treated as an area where the impact of mink could be strong, i.e., an "Impact" area. Two periods were also distinguished: the first ("Before") covered six seasons (1981/1982–1986/1987) when American mink was still not present in most of the country or had just started colonisation of the north, and the second ("After") covered the six most recent seasons (2002/2003–2007/2008) when the mink population in the Impact area was quite stable and at high density as compared to the former period. To make the division reliable, the years between the "before" and "after" periods (1987/1988–2001/2002) were excluded from the analysis, since the abundance of mink in the Impact area during this interval was characterised by intermediate values, and the expansion of this species was still proceeding. The General Linear Model was applied, with annual hunting bags of muskrat as a dependent variable and period (before vs. after) and region (Control vs. Impact) as fixed factors. The interaction between these two factors was also tested. Dependent variable was normally distributed ($p<0.728$ in all cases).

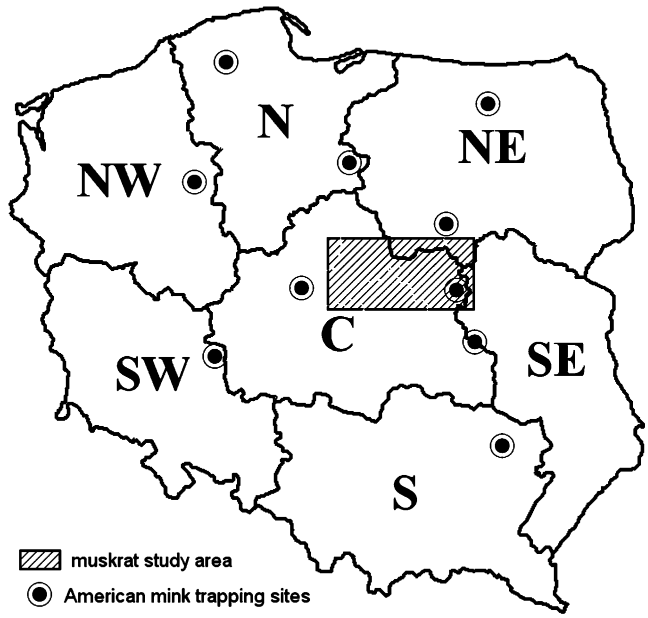

Fig. 1 Map of Poland divided into seven regions, showing the muskrat study area and American mink trapping sites

The abundance of aquatic habitats in the seven regions was analysed using Geographic Information System techniques (ArcView GIS 3.3 ESRI). For each region, the total area of water bodies including lakes, ponds, swamps, periodically flooded terrains and rivers (excluding water courses of width <30 m), was evaluated. Due to the presence of different habitats in particular regions, the total area of water bodies per 1 km^2 was calculated and hereafter used as an index of Aquatic Habitat Availability (AHA) for further statistical analysis.

Results

Data collected in central Poland showed that in 1996–1998 muskrat signs were found at 44% (110) of study sites, while in 2006–2007, this number had fallen to just 7% (17) of sites (χ^2=91.4, df=1, p<0.001; Fig. 2). Ten sites were inhabited by muskrats during both surveys, while seven positive recordings made in 2007 were at sites that were previously negative.

The decline in hunting bags of muskrat was recorded in five districts in the C region (in which all the survey sites were located) from 1,310 (60 muskrats per 1,000 km^2) in 1997/1998 to 524 (24 muskrats per 1,000 km^2) in 2007/2008. The fall in the number of muskrats taken over the last 10 years is relatively small if compared to the decline recorded over a longer period, starting from the beginning of the 1980s. In the whole of central Poland, hunting bags of muskrat declined 11-fold, from a maximum in 1988/1989 (209 muskrats per 1,000 km^2) to a minimum in 2006/2007 (19 muskrats per 1,000 km^2). A significant reduction in hunting bags of this rodent occurred in all regions (Fig. 3). Over the whole country, the number of muskrats taken decreased from 66,416 individuals in 1987/1988 to 4,567 in 2007/2008. Since 1987/1988, the number of muskrats in hunting bags has declined every year with no distinct year-to-year fluctuations.

At the end of the 1980s, when the Polish Hunting Association recorded the largest game bags of muskrat, the number of individuals killed by hunters in three regions (NW, N and NE, that comprise 42.3% of the area of the country) represented 56.5% (1988/1989)—57.9% (1987/1988) of all muskrats taken in Poland. Twenty years later, the number of muskrats taken in the same area comprised only 17% (2007/2008) of the total game bag of this species. The decline in hunting bags of muskrat was most rapid in the north and north-east regions of Poland (Fig. 3). In the north, the number of muskrats killed declined 170-fold, from 15,324 in 1981/1982 (420 muskrats per 1,000 km^2) to just 93 in 2007/2008 (three muskrats per 1,000 km^2); and in the north-east, this number decreased 140-fold, from 14,495 in 1981/1982 (276 muskrats per 1,000 km^2) to 103 in 2007/2008 (two muskrats per 1,000 km^2). Other regions showing a rapid fall in the number of muskrats taken by hunters

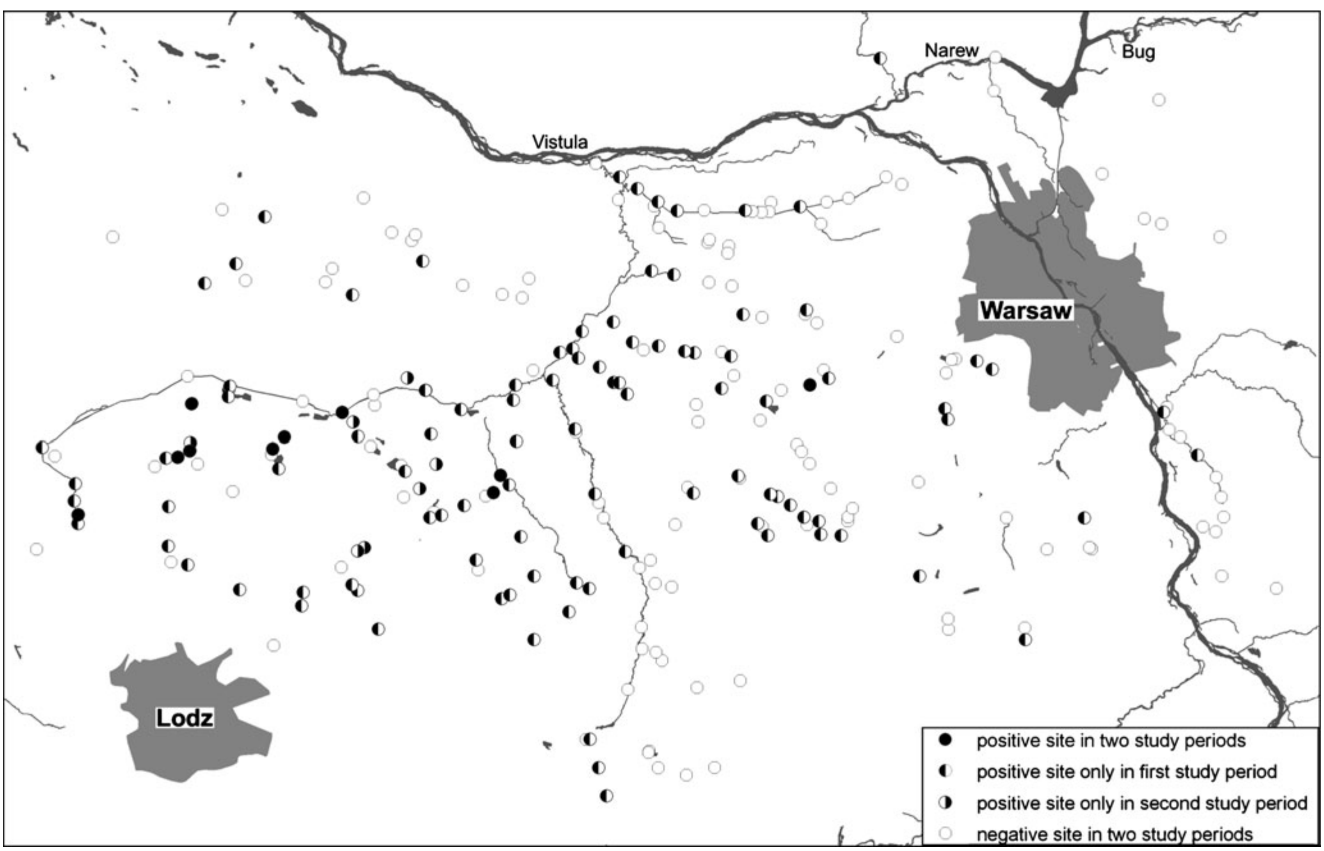

Fig. 2 Field survey of muskrat in central Poland showing the presence/absence of this rodent at each of 249 sites in 1996–1998 and 2006–2007

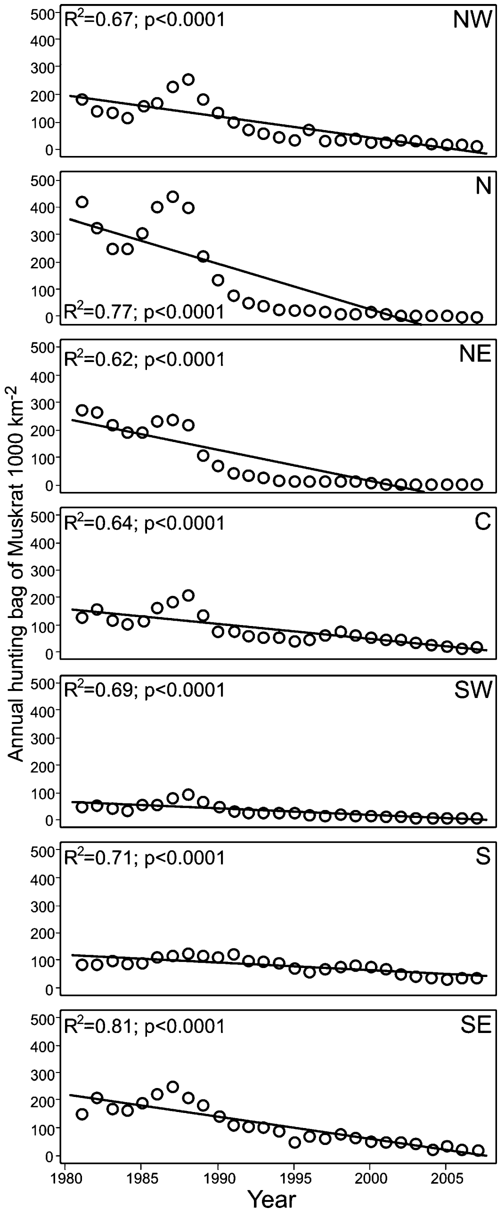

Fig. 3 Hunting bags of muskrat in seven regions of Poland in years 1981–2008

were the south-east and north-west. The region where hunting bags of this rodent declined at the slowest rate was the south. In this part of Poland, the highest number of muskrats killed was recorded in 1988/1989 (128 muskrats per 1,000 km^2), whereas the lowest was in 2005/2006 (34 muskrats per 1,000 km^2). In 1988/1989, muskrats taken by hunters in this region comprised 10.7% of the total Polish game bag of this species; in 2007/2008, this figure had increased to 42.8%.

In the last 6 years, about 43% of American mink taken by hunters in Poland were from the north-east (Fig. 4). The game bags of mink recorded in this region were about 120-fold larger than in the south and about 7-fold larger than in central Poland. The relative abundance of American mink in particular regions of Poland estimated on the basis of game bags from 2002 was confirmed by mink trapping. The highest trapping success and mink densities were recorded in north and north-east Poland (Table 1). No mink were captured at three trapping sites in central, south-west and south Poland.

Comparison of hunting bags of both species in the years 2002–2008 in seven regions of Poland indicated a significant negative correlation between the numbers of mink and muskrats taken by hunters (Pearson correlation, $R=-0.92$; $n=7$; $p=0.003$). Regions recording the largest bags of mink had the smallest bags of muskrat (Fig. 4).

Application of the General Linear Model showed that hunting bags of muskrat depended on both the period ($F=415.05$; $df=1$; $p<0.0001$) and the region ($F=31.95$; $df=1$; $p<0.0001$), and interaction between these two factors was highly significant ($F=87.99$; $df=1$; $p<0.0001$). In the period prior to mink colonisation ("Before", 1981/1982–1986/1987), the mean annual hunting bag of muskrat was nearly 2-fold higher in the Impact area than in the Control area (Fig. 5). Over the last 6 years, the mean annual hunting bags of muskrat in both areas have significantly decreased compared to the numbers recorded at the beginning of the 1980s. In contrast to the "Before" period, the mean annual bag of muskrats in the "After" period (2002/2003–2007/2008) was lower in the Impact area than in the Control area, which indicates that the influx of American mink had a significant effect on muskrat abundance.

The present densities of muskrat in different regions of Poland are inversely related to the availability of aquatic habitats; however, this relationship was positive at the beginning of the 1980s, prior to the mink expansion (Fig. 6). The annual hunting bags of muskrat in particular regions in

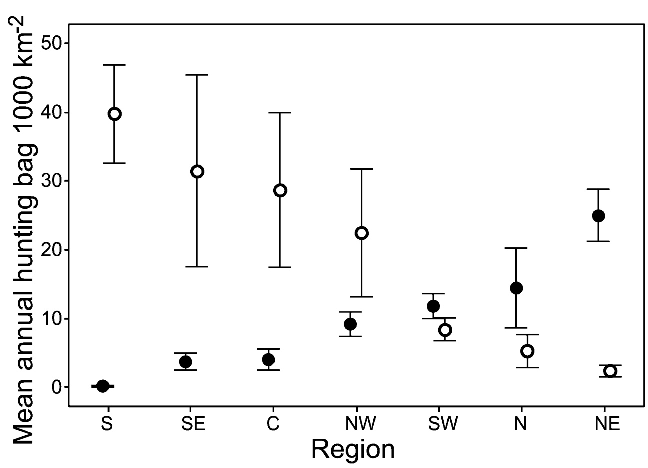

Fig. 4 Mean hunting bags of muskrat (*empty circles*) and American mink (*filled circles*) in years 2002–2008 in seven regions of Poland. *Whiskers* denote 95% confidence intervals for the means

Table 1 Trapping success (*N*/100 trap nights) and densities (*N*/10 km) of American mink in Poland in years 2004–2007

Study area, region	Season	Trap nights	Trapping success	Density
Gwda River, NW	Spring 2007	117	6.8	5.3
Słupia River, N	Spring 2006	89	10.1	9.5
Wel River, N	Spring 2006	69	15.9	8.8
Mazurian Lakeland, NE	Winter 2007	215	7.0	5.4
Narew River, NE	Spring 2004	87	14.9	10.8
Vistula River, C	Winter 2005	49	16.3	8.0
Vistula River, SE	Spring 2007	175	6.9	10.0
Warta River, C	Winter 2006	40	0	0
Milickie Ponds, SW	Spring 2006	76	0	0
San River, S	Winter 2007	91	0	0

the "Before" period did not depend on the year (included as a random factor in the General Linear Model; $F=0.56$; $df=5$; $p=0.730$) but were positively correlated with the AHA index (included as a covariate, $F=16.12$; $df=1$; $p<0.0003$). However, in the "After" period, annual bags of muskrat were negatively correlated with the AHA index ($F=21.43$; $df=1$; $p<0.0001$). The between-year variation was also insignificant during this period ($F=1.75$; $df=5$; $p=0.148$).

Discussion

Hunting bags are considered to be an indirect and not always precise method of estimating game numbers (Ranta et al. 2008); however, they are frequently used to study population dynamics (Merli and Meriggi 2006; Schley et al. 2008; Seläs 2006). The results of field studies on muskrat distribution in central Poland confirmed the reliability of hunting bags in estimating population trends. In years 1996–2007, the number of recorded muskrat-positive sites, as well as game bags of this rodent, declined in this region. However, the population decline based on the number of harvested animals was more rapid than the decrease in the number of sites inhabited by muskrats.

At the beginning of the 1980s, muskrat densities in different regions of Poland depended mostly on the availability of optimal habitats. Muskrat densities are known to be related to habitat quality. Le Boulengé and Le Boulengé-Nguyen (1981) showed that muskrat densities recorded in different localities can vary greatly, from less than one to over 80 individuals per hectare. Artimo (1960) found that

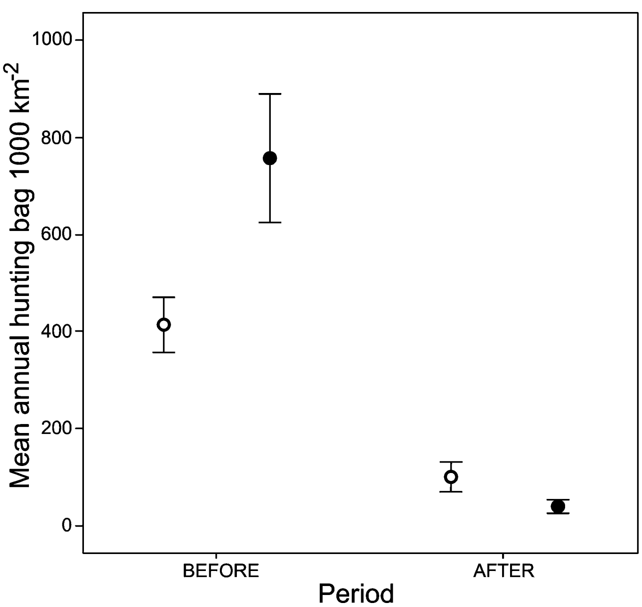

Fig. 5 Mean annual hunting bags of muskrat in the Control area (*empty circles*) and Impact area (*filled circles*) for the periods before (1981/1982–1986/1987) and after (2002/2003–2007/2008) mink expansion in Poland. The Control and Impact areas covered regions with small and large hunting bags of mink during the last six seasons, respectively (presented in Fig. 4). *Whiskers* denote 95% confidence intervals for the means

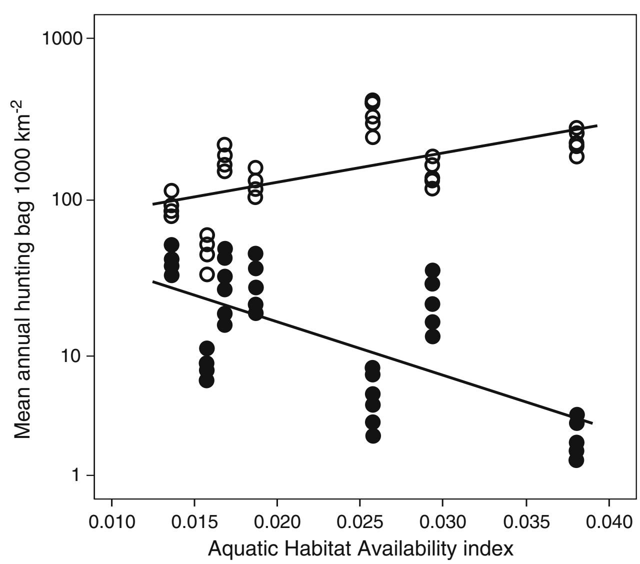

Fig. 6 Annual hunting bags of muskrat per 1,000 km^2 in Poland in relation to the Aquatic Habitat Availability index. Each *circle* represents the hunting bag for 1 year and region. *Empty circles* denote the "before" period and *filled circles*, the "after" period

after the successful expansion of muskrat in Finland, the highest population densities were recorded in eutrophic watercourses in regions with intensive cultivation. In water systems of low productivity, the shortage of food limited the increase in muskrat populations (Artimo 1960). Similarly in Poland, muskrat populations reached their highest densities in regions with well developed eutrophic water systems: the lakelands in the north of the country. Since the 1980s, it is unlikely that the capacity of these optimal habitats in northern Poland has changed significantly in comparison with other regions. Muskrats are highly vulnerable to changes in water level and habitat conditions, and their populations undergo significant annual mortality which may reach 80% to 90% (Le Boulengé and Le Boulengé-Nguyen 1981; Simpson and Boutin 1993). Water deficiency in Poland affects mainly the southern and central parts of the country but not the north (illustrated by the AHA index). Variations in water level occur mainly in rivers and marshes and are not very common in eutrophic lakes. These facts may explain the relatively low densities of muskrats in southern Poland, where resources are scarce and unstable (water levels in mountain and highland rivers change rapidly). In addition, water quality has actually improved since the 1980s. Thus, we conclude that in recent decades, changes in habitat quality are unlikely to have led to the drastic decline in muskrat populations, at least in northern Poland. However, increasing water deficiency in some regions may have, directly or indirectly, affected muskrat mortality, which is known to increase at times of reduced water levels and in suboptimal habitats due to higher predation (Clark and Kroeker 1993; Soper and Payne 1997). In some areas of Poland (e.g. the central region), muskrat numbers appear to have been affected by the cumulative effect of negative changes in their habitat and increased predation by mink.

The negative correlation of muskrat and mink population dynamics (game bags) in various regions of Poland indicates that mink predation is one of the most important factors affecting muskrat numbers. This suggestion is confirmed by the BACI analysis and is in agreement with the conclusion of Brzeziński and Marzec (2003) based on the analysis of questionnaires from Polish hunters (collected in 1998) regarding the abundance and dispersion of American mink. Since that time, the expansion of mink has continued in many regions with the concomitant decline in local muskrat populations.

In North America, mink is the main muskrat predator and is considered to be specialised to prey on these rodents. However, Errington (1963) concluded that the significance of mink in reducing muskrat populations has been overestimated because the majority of animals killed by mink are usually individuals inhabiting suboptimal habitats, and mortality among this group—not related to predation—is always high. The more recent studies of Erb et al. (2001) and Viljugrein et al. (2001) showed that muskrat and mink populations in Canada undergo 8–9-year cycles, which are synchronous, or muskrat cycling is 1–2 years ahead of the mink. These authors suggest that these correlated oscillations of the two species reflect a typical predator–prey relationship (the presence or absence of a 1–2 year lag may reflect how strong this relationship is—see Viljugrein et al. 2001). The typical muskrat and mink cycles occurring in North America have not been observed in Europe, where both have expanded as invasive species. Assuming that hunting bags reflect changes in the population numbers of muskrat, some multiannual oscillations of this species have been recorded in Poland but only during the period of muskrat population growth (Nowak 1966). This, however, was before the invasion of mink. Mink populations started to grow rapidly in Poland during the first half of the 1980s, first in the north-east and north-west, and later in other regions of the country (Brzeziński and Marzec 2003). Since that time, muskrat populations in the areas invaded by mink started to decline, and no significant fluctuations in their numbers were observed. This decline has been continuous for at least 20 years, and in many areas of northern Poland muskrat populations are now extremely small or extinct.

The population of American mink in Poland is still expanding (Brzeziński and Marzec 2003), and mink densities in some regions are relatively high. This is why the impact of mink on populations of several prey species, which are not adapted to mink predation, can be highly significant. Studies in Europe have shown the significant impact of mink on some species of waterfowl (Craik 1997; Ferreras and Macdonald 1999; Nordström et al. 2002) and rodents such as the water vole (Aars et al. 2001; Carter and Bright 2003; Woodroffe et al. 1990). Muskrats are the natural prey of mink in North America where the two species coevolved. However, in areas where muskrats have not previously faced mink predation, their anti-predator adaptations are probably not well developed, leading to significant population decline when they contact invading mink (Balerstet et al. 1990; Soper and Payne 1997). This scenario may have been observed recently in Poland. Bartoszewicz and Zalewski (2003) studied the diet of mink in north-western Poland in the late 1990s and found muskrat to be an important prey. On the other hand, Brzeziński (2008) found that over the same period, muskrats were not predated by mink in north-eastern Poland, probably because their numbers in this region were already very low (see Fig. 5). Thus, we may expect that in the immediate future the impact of mink on muskrat populations will continue to be strong, and oscillations, typical for North America, will not occur.

However, it is difficult to predict the dynamics of muskrat populations in the longer term when mink densities have stabilised and muskrats have adapted to the presence of this predator.

Despite the evidence of mink impact on muskrat populations, other ecological factors such as the availability of food, diseases, parasitism and predation by other carnivores and raptors should not be ignored (Le Boulengé and Le Boulengé-Nguyen 1981)—decline in muskrat numbers has also been recorded in regions of Poland lacking mink or with very low densities of this carnivore. Predation by fox (*Vulpes vulpes*) should be considered as an important factor affecting muskrat populations (Danell 1985; 1996). In recent years, foxes have increased in number, probably due to the rabies eradication programme; the total hunting bag for this species increased from 95,367 in 2000/2001 to 136,192 in 2006/2007. However, the increase in fox densities has been observed throughout Poland and cannot be related to regional differences in the decline in the muskrat population. Thus, it is highly likely that foxes could accelerate the decline in muskrat numbers, but their predation was not the main factor leading to the deterioration of many local muskrat populations. Nothing is known about muskrat diseases in Poland that may contribute to the reduction in muskrat numbers, as was recorded in Sweden during an outbreak of tularaemia (Danell 1996). Genetic monomorphism of the European population may increase a possible susceptibility of the muskrat to diseases and parasites (Zachos et al. 2007).

The muskrat has successfully colonised many European countries, including Poland. Danell (1996) proposed that this colonisation in the first half of the twentieth century was possible because the muskrat has many attributes of a successful invading species, and its target environments in Europe were open to invasion by this semi-aquatic rodent. Intensive human persecution slowed the muskrat expansion across Europe but could not exterminate this species (the only exception is in the British Isles). In contradiction to Danell (1996), we suggest that the successful expansion of muskrat in many regions of Europe was possible due to the lack of effective muskrat predators, particularly the American mink. The expansion of muskrat preceding that of the American mink seen in Poland has also occurred in other countries such as Finland (Artimo 1960; Kauhala 1996). We will never know how muskrat expansion may have developed in the presence of American mink, although population trends of both species observed in recent decades suggest that invasive mink can successfully reduce muskrat numbers. This conclusion is consistent with the results of Soper and Payne (1997), who found that predation by introduced mink of muskrats, which were not adapted to this predator, caused the population to decline.

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