Introductions of aquatic rodents: lessons of the muskrat Ondatra zibethicus invasion

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The muskrat *Ondatra zibethicus* is one of the semi-aquatic rodents that has been introduced into many areas of the world. It is regarded as a most successful vertebrate invader. In northwestern Europe, it was introduced to Finland in 1919 and to the Kola Peninsula in 1931. From these areas, it spread 'naturally' to Sweden and Norway, respectively. Here the history of the introduction, dispersal, population development, impact on plant communities, impact on man, and indirect and direct effects on other animals in northwestern Europe are reviewed. The biological features of the muskrat are discussed in relation to the attributes of other vertebrates that are regarded as successful invaders.

Key words: muskrat, Ondatra zibethicus, introductions, invasion, dispersal, population dynamics, impact on biota

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World-wide, almost 200 mammalian species have been introduced to regions in which they did not occur previously (Ebenhard 1988). The 10 most commonly introduced mammals are common rabbit *Oryctolagus cuniculus*, Norway rat *Rattus norvegicus*, ship rat *Rattus rattus*, house mouse *Mus musculus*, Polynesian rat *Rattus exulans*, and the domesticated cat *Felis catus*, dog *Canis familiaris*, cattle *Bos taurus*, goat *Capra hircus* and pig *Sus scrofa*. These 10 species are involved in 54% of the 788 introductions reviewed by Ebenhard (1988). However, in terms of number of species, the rodents are slightly underrepresented while the even-toed ungulates and predators are overrepresented. Among the rodents are three semi-aquatic species that belong to the group of introduced mammals, i.e. Canadian beaver *Castor canadensis*, muskrat *Ondatra zibethicus* (Linnaeus, 1766) and nutria *Myocastor coypus* (Ebenhard 1988). The most detailed and extensive knowledge existing on these semi-aquatic rodents concerns the muskrat and its impact on foreign biota. For this reason the muskrat is used as an example in this review.

The aim of this paper is to describe the history and results of muskrat introductions, as well as dispersal rates, population development and the impact of muskrats on their habitats and biota in northwestern Europe. Furthermore, I discuss why the muskrat has been such a successful invader in a variety of habitats.

The muskrat

The muskrat is originally a North American, semi-aquatic rodent. It belongs to the family Muridae (subfamily Arvicolinae) and is the only species within the genus *Ondatra* (Musser & Carleton 1993). It has a 'rat-like' appearance but is actually closely related to voles *Microtus* spp. and lemmings *Lemmus* spp. On average, adult animals weigh slightly more than one kg. The body length is around 50 cm and the tail is approximately 25 cm (Banfield 1974). The muskrat is easily recognised by its relatively long tail which is naked and laterally flattened. The species can survive in many habitats ranging from subtropical rivers and coastal marshes to arctic tundra and deltas (Errington 1963).

The history of introductions and their results

The muskrat has been introduced into many areas of the world, especially in Europe and Asia (e.g. Hoffmann 1958), but also in South America (Hoffmann 1985). In 1905, the introductions into Europe were initiated. The first animals were released on a private estate about 40 km southwest of Prague (Bohemia, the Czech Republic) in Central Europe and from there they spread to neighbouring countries (Hoffmann 1958). The spread of the species in Europe was facilitated by both intentional releases and escapes from fur farms. Various efforts to reduce the spread or exterminate the muskrat were insufficient. However, one exception is the British Isles where the muskrat was introduced in 1927 for fur farming and escaped, but was exterminated in 1939 (Warwick 1940, Hoffmann 1958).

In the former Soviet Union, muskrats were introduced in 1928 (Hoffmann 1958). The animals were released mainly in areas with low agricultural activity because of the risk of damage to dams and other constructions in water. During 1928-1945 ca 80,000 animals were set free in many different regions.

Here, I will concentrate on the spread of the species in northwestern Europe (defined as Norway, Sweden, Finland and the Kola Peninsula of the former Soviet Union). In this area there were two nuclei from which further spread originated: Finland and the Kola Peninsula.

For financial reasons, Finland imported ca 1,100 muskrats from Germany, Czechoslovakia and North America (Artimo 1960). Muskrats were released in a total of 293 localities all over Finland from 1919 and onwards. Within 35 years (1920-1955) muskrats had established in almost all available habitats, with the exception of those in the northernmost parts of Finland.

From northern Finland muskrats spread into Sweden. Around 1940 muskrats occurred on the Finnish side close to the river Torne which constitutes the border between Finland and Sweden, and in 1957 the species had fully occupied the lower region of the border river (Artimo 1960). A couple of muskrats were shot at Salmis on the Swedish side of the river in the spring of 1946 (Anonymous 1984). The village of Salmis is situated ca 2 km from the Finnish border; this means that the species most likely passed the border around 1945. Liljeström (1954) reported an illegal transport of muskrats in the upstream reaches of the Torne around 1943. Even though we have only scattered information on the early history of the muskrat in Sweden, the muskrat most likely belonged to the Swedish fauna in 1945, and definitely did so in 1950. The further spread of the muskrat in Sweden has been studied by Marcström (1964) and Danell (1977a). In 1996 muskrats occur as far south as Husum in Sweden which is ca 25 km east of Örnsköldsvik (Gradin 1996) and the spread in Sweden continues southwards.

On the Kola Peninsula (Lapland Nature Reserve) the introductions started in 1931 (Semjonov-Tian-Sjanskij 1987). In total, ca 1,000 muskrats were released on the Kola Peninsula during 1931-1936. Just before 1950 muskrats occurred all over on the peninsula (Semjonov-Tian-Sjanskij 1987).

It seems quite natural that the species, sooner or later, would disperse into northern Norway, which shares a border with Russia at the Barents Sea, from the Kola Peninsula. Around 1960 there were observations of 'possible' muskrats in the river Alta area in Troms, northern Norway (Vik 1963), but the first specimen was not recovered until 1969 when a muskrat was captured alive in Smalfjord at Tana (Lund & Wikan 1995). In 1970, another specimen was collected from Jarfjord in the South Varanger district in Finnmarken (Pedersen 1970). Between 1980 and 1988 there were very few observations of muskrats in Norway (Lund & Wikan 1995). Since 1988 there has been a rapid population increase in Sör-Varanger, and today the muskrat has spread to almost every part of the municipality.

Dispersal rate of the species

The central European muskrat population was established through the introduction of five individuals in Bohemia in 1905. Between 1960 and 1970 the population originating from these individuals and the population developing in Belgium and France (escapes from fur farms) merged (van den Bosch et al. 1992). After this merger the picture of muskrat dispersal in central Europe became quite complicated. Therefore, van den Bosch et al. (1992) narrowed their analyses of dispersal rates to the period 1905-1960. Because large trapping programmes had been started in central Europe around 1925-1930 they subdivided this period into two periods (1905-1930 and 1930-1960). For the two periods, the dispersal rate was ca 11 and 5 km per year, respectively (Table 1). This means that the disper-

Table 1. Spread of muskrat in Central Europe, Finland and Sweden. For Sweden data are given for dispersal along the coast of the Bothnian Bay and Bothnian Sea only.

Region	Time period	Average dispersal (km/year)	Source
Central Europe	1905-1930	11	van den Bosch et al. 1992
Central Europe	1930-1960	5	van den Bosch et al. 1992
Finland	1920-1960	10-20	Artimo 1960
Sweden	1945(1950)-1963	7-(9)	Marcström 1964
Sweden	1963-1974	5	Danell 1974
Sweden	1974-1994	11	This article

sal rate was reduced during the period with more intense trapping.

For Finland, Artimo (1960) described the history of the spread of the muskrat after 1920. In northern Finland, the spread has been distinctly slower than in southern Finland. The spread has varied within limits of 4-120 km per year, but usually muskrats have spread at a rate of 10-20 km per year (see Table 1).

In Sweden, there have been and still are excellent possibilities of studying the dispersal rate of the muskrat southwards in the country with little or no human interference. Trapping has been insignificant due to the low price of muskrat furs and the banning of leghold traps. Furthermore, the muskrat has not been regarded as a 'pest' animal in Sweden and therefore there have been no campaigns to reduce their number. Furthermore, the spread of the species has taken place almost without any human interference - only one case of illegal transport has been reported (Liljeström 1954) but most likely this did not affect the overall distribution of the species. The initial spread of the muskrat in Sweden along the coast was around 10 km or less per year (see Table 1); the dispersal in the inland areas was slower. During the last 20 years the dispersal tends to be somewhat faster than during the first 25-30 years. A more rapid dispersal in southern and more productive areas, where the ice-free period is longer, can be expected. I expect the further spread in Sweden to take place at a rate slightly higher than 10 km per year, if the spread of the animals is not facilitated by humans.

For Norway, there are no recent mappings of the muskrat distribution and no analyses of the dispersal rate during different periods. The species still occurs in areas with quite unfavourable habitats where population density is very low.

Population development

Because the muskrat in Sweden has been only marginally affected by trapping and translocation there have been and still are quite unique opportunities to follow the population development at various sites along the distribution route towards the south.

The fox *Vulpes vulpes* and mink *Mustela lutreola* are the main mammalian predators on muskrats in Sweden (Marcström 1964). The predation by mink is less obvious than the predation by fox. During winter, foxes regularly patrol the frozen lakes and sometimes make successful attempts of catching a muskrat, especially in late winter/early spring or after mild-weather periods when the muskrats leave their houses or when it is possible to dig out their houses. Even in summer, foxes regularly visit muskrat houses in search for litters and they can be quite

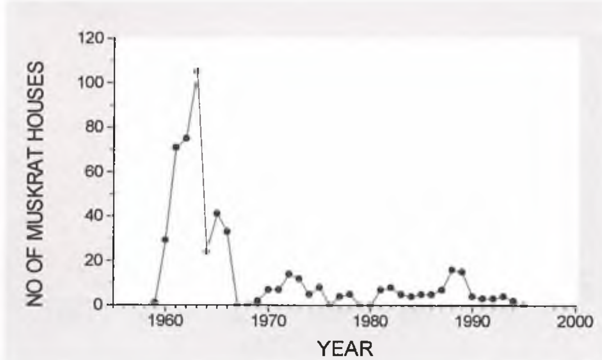

Figure 1. Number of muskrat winter houses at Lake Puostijärvi (66° 20' N; 23° 24' E) in northern Sweden. The lake was colonised by the muskrat in 1959 when a single house was found. Since 1959, the number of winter houses has been counted in early winter every year.

efficient in taking young muskrats (Danell 1978). Also large predatory birds take muskrats, but most likely on a quite occasional basis (Marcström 1964).

Within the northern range of their distribution area the muskrats have been relatively healthy and unaffected by diseases or parasites (Marcström 1964). However, in the early 1970s muskrats in northern Sweden died during an outbreak on tularaemia.

Here data on the number of muskrat winter houses are given for three muskrat populations established in 1959 (Puostijärvi; Fig. 1), 1963 (Lake Sladan; Fig. 2) and 1975 (Lake Osträsket; Fig. 3) in northern Sweden at 64-66°N. Within the first 5-10 years after the first observations the populations attained a distinct peak at two of the sites (Puostijärvi and Ostträsket) and a population size of that magnitude has never since been attained. This response can be classified as an 'overshoot' according to Caughley (1970). The population development at the third site (Sladan) partly follows the same pattern with an 'overshoot' in the early establishment phase, but another one later on.

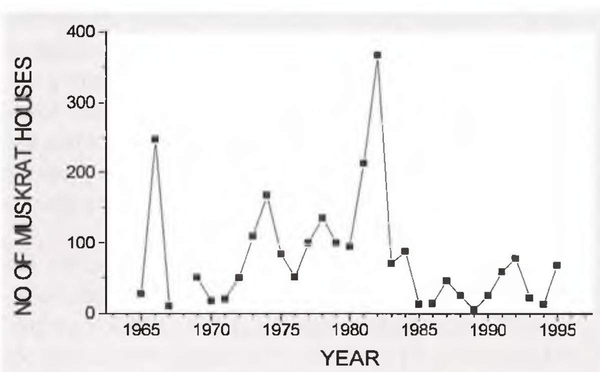

Figure 2. Number of muskrat winter houses at Lake Sladan (65° 55'N; 22° 25'E) in northern Sweden. The lake was colonised by the muskrat in 1963, and since 1965 the number of winter houses has been counted in early winter every year (except for 1968).

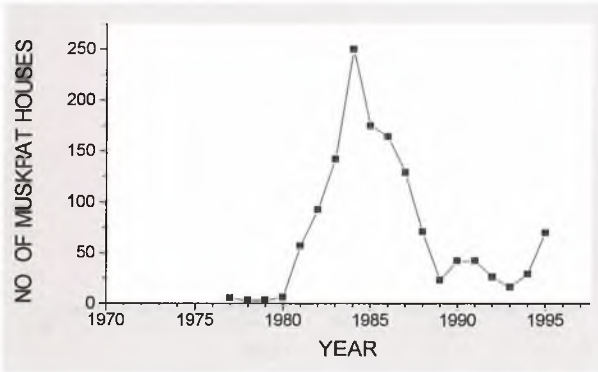

Figure 3. Number of muskrat winter houses at Lake Ostträsket (64° 55'N; 21° 03'E) in northern Sweden. The lake was colonised by the muskrat in 1975, and since 1977 the number of winter houses has been counted in early winter every year.

For this third site, Danell (1978, 1985) reported strong interactions between voles (*Clethrionomys* spp. and *Microtus* spp.), red fox, and muskrat, i.e. the predation pressure by fox on muskrat litters was highest during years with low abundance of voles and low during years with high abundance of voles. The muskrat population responded by a peak one year after the vole peak and was thus closely linked to the microtine rodent 'cycle' of 3-4 years. In 1975, the red fox in the area was affected by a serious form of sarcoptic mange, which reduced the fox population (Danell & Hörnfeldt 1987), and consequently the muskrat population responded with a peak in 1982. During the last 10 years the fox has gradually recovered and parallel with this the muskrat population has been kept at a lower level. However, a broader analysis of the impact of the sarcoptic mange among foxes and its secondary effects on prey species is in progress.

Feeding and house-building

Feeding on aquatic plants and house-building are the two main activities that will noticeably affect the habitat of the muskrat. As the animals do not hibernate, feeding occurs throughout the year. During the ice-free season feeding is spread over larger areas, but during winter when the habitats are ice-covered feeding activities are heavily concentrated to the close vicinity of the houses or the entrances of burrows.

House-building is concentrated in the autumn, but occurs throughout the ice-free season of the year. The muskrat builds houses of plant material and mud which are collected very close to the house. The largest houses are often used by a group of animals, while the smallest ones are used as feeding sites and for breathing as well as shelter during travels of the animals within their territory. In between the largest and the smallest houses there is a whole gradient of houses of different sizes. It is neither possible nor meaningful to try to separate the houses into distinct size classes with different use.

In northern areas there are often great fluctuations in water levels during the year due to spring floods after the snow melt. In such areas, houses are often destroyed and need to be rebuilt every spring.

Some sites within the habitat are more frequently occupied by houses year after year than others. This strong site tenacity of the muskrat for house-building, the low persistence of the houses and the concentration of foraging movements when the habitat is ice-covered lead to a concentrated, and sometimes heavy impact of the muskrat on the vegetation in shallow waters.

In habitats unsuitable for house-building muskrats may dig burrows if the material of the shoreline permits digging.

Impact on habitat structure

The muskrat has a great potential to reduce vegetation. There are numerous reports on this topic from both North America and Europe. The general opinion on the impact of muskrats on their habitat is mixed, especially in northern Europe. On the one hand, the animal is regarded as a positive factor because it creates openings in dense vegetation stands and it prevents lakes from being overgrown by vegetation. On the other hand, it has been blamed for destroying valuable vegetation and creating mud-flats. Depending on human interest in the development of the particular wetland the muskrat may be regarded as a valuable element or as a 'pest' species.

In order to predict the impact of the muskrat on its habitat, I propose that an analysis should include the productivity of the habitat and also take into consideration if the muskrat population is in the invasive or the post-invasive phase (Table 2). In poor habitats the plants have a lower potential to recover after herbivory than plants in nutrient-rich habitats. Furthermore, during the invasion phase extremely high muskrat densities may be reached for a few years, but most likely they will decline after the invasion phase. Therefore, we may expect the most severe impact to be found in the poor muskrat habitats during the invasion phase. The least impact will be found in very

Table 2. Impact of the muskrat on two wetland habitat types. Important factors for the outcome include the productivity of the site and whether the muskrat population is in the invasion phase or not. +++ = high impact; + = low impact. For further details see text.

Habitat type	Invasion phase	Post-invasion phase
High productive habitat	++	+
Low productive habitat	+++	++

productive habitats when muskrats have occurred on the locality for decades.

In waters with poor stands of helophytes heavy reductions in these stands have been reported. For example, a study of 38 small lakes in southern Finland showed that since the late 1940s stands of some plants that used to be dominant, especially *Schoenoplectus*, *Equisetum* and *Nymphaea* have decreased considerably or even become extinct (Toivonen & Meriläinen 1980). However, it must be pointed out that these changes may have been caused by other factors than the muskrat. The introduction of muskrats to the former Soviet Union was followed by strong impact of the muskrat on emergent vegetation (Chashchukhin 1975), especially in the northern parts of the muskrat's distribution range. For example, in Western Siberia and Kazakhstan thousands of hectares of *Phragmites* stands were exterminated.

In poor habitats which have been overexploited by the muskrat during the invasion phase one common result is that the muskrat abandons the site and allows the vegetation to recover (Artimo 1960, Marcström 1964). In most situations, the initial changes caused by the muskrat are reversible within a few years. One exception is sites where the elimination of the vegetation in combination with currents has resulted in relocation of fine sediment from shallow to deeper areas of the bottom. With the fine sediment gone, the recolonisation of emergent vegetation will be significantly delayed.

There are few quantitative studies on the total reduction of plant biomass in muskrat habitats. In a Czechoslovakian lake, muskrats reduced the annual production of *Typha latifolia* by 5-10% (Pelikan et al. 1970). In a northern Swedish lake, Danell (1979) estimated a removal of ca 4% of the *Equisetum* stands following a population peak. These two studies performed in productive habitats indicate that the overall impact of the muskrat is relatively small.

Even though the muskrat eliminates only a small proportion of the yearly production of plant biomass this will cause a significant structural change in the vegetation. The concentrated house-building and feeding lead to overutilisation of numerous, but relatively small 'hot spots' where open-water areas are created in otherwise dense emergent vegetation. These spots are often connected by a network of narrow 'channels'. The overall effect is an increase in the edge between open water and vegetation. For one lake in northern Sweden (see above, Danell 1979) I estimated that there were ca 160 such small patches per hectare and that the combined perimeter length was about 1.5 km. Most of the patches were very irregular in shape, each with a long perimeter in relation to its area.

There is still only limited knowledge of the effect of the muskrat on ecosystem processes in wetland habitats. The opening up of dense vegetation beds creates a mosaic of sites with different light and temperature climates, where ecological processes proceed at different strengths and rates. Therefore, we may expect numerous microgradients in the various resource variables to affect ecosystem processes such as decomposition and nutrient cycling. Furthermore, it has been demonstrated that the litter from muskrat mounds has significantly higher densities of microbes than the marsh floor (Wainscott et al. 1990) suggesting that the mounds act like the compost piles of organic gardens in providing a microenvironment conducive to enhanced microbial growth and accelerated decomposition. The effect of the muskrat on ecosystem processes in wetland habitats definitely needs further study. The results found so far indicate that the presence of muskrats increases the heterogeneity of the wetland both structurally and functionally.

Impact on plant succession

The arriving muskrats start a cascade of plant succession in the wetland. The open-water areas created are colonised by plant species with weak competitive ability within stands of emergent hydrophytes. Such species include various floating-leaved and submerged plant species of the genera *Myriophyllum*, *Potamogeton* and *Sparganium* (Danell 1977b, Toivonen & Meriläinen 1980). If the open-water patches later are abandoned by the muskrat the growth of these plant species is further stimulated. However, the emergent plants successively grow into the lost areas and slowly outcompete the floating-leaved and submerged plant species (Danell 1977b). Because numerous new patches are created and abandoned by the muskrat over time, the muskrat creates a diverse set of patches in different stages of succession (Danell 1977b). This diversification is further increased by the large between-year fluctuations in the muskrat populations.

The vegetation on muskrat houses differs quantitatively, but not qualitatively, from the vegetation in the surrounding areas (Kangas & Hannan 1985).

The muskrat can be regarded as a 'keystone' species in most wetland habitats with abundant water. This rodent species increases the diversity of the habitat structure and plant species richness at intermediate disturbance levels. Muskrats also have the potential to destroy the vegetation and reduce the abundance of some plant species when becoming too numerous. Total elimination of some plant species does not seem likely, however, even though it must be pointed out that most of the knowledge on the impact of muskrat on plant cover has been gained from productive habitats.

Direct effect on other animals

Muskrat is a poor predator on fish, birds and mammals. However, if muskrats find dead or helpless animals, e.g. fish, they may take these. There is no doubt that muskrat is a predator of freshwater mussels, e.g. *Anodonta* and *Unio* species (Brander 1951, Marcström 1964, Akkermann 1975). The relations to crayfish have not been studied, but when other foods are scarce the muskrat may reduce crayfish stocks considerably (Sundblom 1964).

Impact on man and his activities

The muskrat only occasionally affects humans directly. This occurs in situations when the animals are cornered. They defend themselves vigorously and may even attack humans.

By making tunnels in the shores muskrat can destroy dams and other man-made structures close to the water. These damages were of great concern in areas densely populated by humans and during the time when buildings were of a weaker construction than they are nowadays. The extent of the damage in western Europe has been reviewed by Doude van Troostwijk (1976). For northwestern Europe there are, at present, few reports on damage caused by the muskrat. Still, it is quite an experience to fall into the water through the undermined shoreline.

Muskrats are sometimes accused of damaging fish traps (Marcström 1964).

Indirect effect on other animals

The habitat of the muskrat in northwestern Europe partly overlaps the habitats of native semi-aquatic herbivores, e.g. water vole *Arvicola terrestris*, root vole *Microtus oeconomus* and beaver *Castor fiber*. Only for the water vole is there some evidence of competition with the muskrat, i.e. a negative correlation was found between the abundance of muskrat and water vole (Zejda 1976). On the other hand, Doude van Troostwijk (1976) reports a positive correlation between trapped numbers of water voles and muskrats.

In well-vegetated and productive wetlands and lakes, the muskrat may be a positive factor for waterfowl by opening dense vegetation stands, thus creating new feeding areas with rich floating-leafed and submerged vegetation, often associated with a rich invertebrate life. On the other hand, reduction of vegetation in localities where the plant cover already is sparse will have the opposite effect.

Muskrat houses are used by a variety of vertebrates for shelter, nesting, foraging and getting out of the water. Kiviat (1978) listed such vertebrate species and Hoffman (1982) recorded 17 species of birds using muskrat lodges. Reindeer *Rangifer tarandus* has been observed to feed on muskrat houses in northern Sweden during winter (pers. obs.). This has also been reported for barren-ground caribou *Rangifer tarandus groenlandicus* in Saskatchewan (Kelsall 1970). The burrowing of muskrats can be positive for other animals using burrows, e.g. mink.

Why has the muskrat been such a successful invader?

Holdgate (1986) formulated three central questions about invasions: 1) What attributes of a species make it capable of invading and becoming established in new habitats? 2) What features of a receiving habitat (physical or biological) make it prone to invasion? 3) What management strategies are appropriate to control the invading species? The muskrat has evidently successfully colonised north-

Table 3. Attributes of successful vertebrate invaders (excluding fish) adapted from Ehrlich (1989) and Brown (1989) and how these apply to the muskrat.

Attribute	Successful invaders in general	The muskrat
Large native range	+	+
Abundant in original range	+	+
Vagile	+	+
Broad diet	+	+
Short generation lines	+	+
Much genetic variability	+	?
Gregarious	+	+
Female able to colonise alone	+	+
Larger than most relatives	+	+
Associated with man	+	-
Able to function in a wide range of physical conditions	+	+
Able to colonise man-made habitats	+	+

Table 4. Attributes of environments/communities prone to invasion of vertebrates (modified after Brown 1989) and evaluation of how these apply to the muskrat.

	Invasions in general	Muskrat invasion
Isolated environments with a low diversity of native species	+	not known[1]
High similarity in the physical and biological environment between source and target areas	+	+
Exotics and native species differ in niche use	+	+

[1] The muskrat has been introduced to mainland localities only in northwestern Europe.

ern Sweden and it might be interesting to discuss whether the muskrat has some features that may explain this colonisation and whether the habitats colonised have some special features that make them prone to colonisation. However, it is difficult to judge if the success of the muskrat is greater than what can be expected from other species. In order to make this judgment we would have needed simultaneous introductions of other species.

Ehrlich (1989) pointed out some attributes of successful invading vertebrates and concluded that such species often show a "broad ecological amplitude". The muskrat has the majority of these attributes, e.g. large native range, high abundance in original range, high vagility, broad diet, relatively short generation time, gregariousness (to some extent), the impregnated female can colonise alone, larger size than most relatives, and is able to function in a wide range of physical conditions. Furthermore, the muskrat has successfully invaded man-made habitats, a valuable attribute pointed out by Brown (1989) (Table 3). However, the muskrat is not associated with man and we do not yet have enough information to conclude whether the muskrat has much genetic variability or not relative to other species. In addition to the positive attributes of the muskrat, it has the capacity to spread over land as well as along and across watercourses and thus it avoids some of the barriers that terrestrial animals normally are affected by.

The target environments/communities in northwestern Europe were quite prone to invasion by muskrats (Table 4). The environments colonised by the muskrat and their native environments have great similarities in climate and vegetation (Artimo 1960). There were also similarities in the predator fauna (made even more similar through the introduction of the American mink) between the native and the receiving habitats. Furthermore, Pietch (1970) suggested that the quick dispersion of the muskrat throughout Europe could be ascribed to the fact that its '-niche' was unoccupied. However, this hypothesis is difficult to test in the field. In most cases we are unable to recognise a vacant niche except by carrying out tautological experiments of introducing a species and seeing if it becomes established (Crawley 1986). Doude van Troostwijk (1976) found that no other species than the muskrat use the various common elements to the same degree as the muskrat. Artimo (1960) and Danell (1977a) argued along the same lines.

The introductions of animals into various environments are some of the most important field experiments ever carried out in ecology (Crawley 1986), and they have provided valuable insight into the biological processes of biological invasions. Still, we are very far from being able to process the kind of ecological sophistication that might allow us to make predictions about the probable outcome of a particular proposed introduction (Crawley 1986). On the other hand, ecologists can make powerful and wide-ranging predictions about invasions in general (Ehrlich 1989). The lessons of the muskrat have contributed substantially to our ecological knowledge of the ecology of vertebrate introductions.

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