Wildlife introductions to mammal-deficient areas: the Nordic countries

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Introduced mammals and birds have had a high rate of success in the Nordic countries. Out of 18 species new to the area, 14 (78%) have established a population in at least one country. American mink *Mustela vison*, raccoon dog *Nyctereutes procyonoïdes*, muskrat *Ondatra zibethicus*, white-tailed deer *Odocoileus virginianus*, Canada goose *Branta canadensis* and pheasant *Phasianus colchicus* have been the most successful exotics. Ecological effects caused by the newcomers include: displacement of European mink *Mustela lutreola* and beaver *Castor fiber* by American counterparts, changes in aquatic vegetation patterns caused by muskrat grazing, and locally heavy predation pressure on colonial waterbirds by the American mink. From now on, introductions of new species should be avoided, at least until proven harmless.

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Although often detrimental, introductions of new wildlife species are interesting, at least in two respects. First, they provide a large-scale experiment concerning general community structure, such as species saturation or naiveté (Diamond & Case 1986). Secondly, they may tell us something about effects of individual species on ecosystem properties (Vitousek 1986).

Animal introductions to the Nordic countries are special because here newcomers face a relatively young community. The Ice Age wiped out life from most of the area, and, especially since the formation of the Baltic Sea (Eronen & Ristaniemi 1992), the area has been relatively difficult to colonise, at least for terrestrial mammals. A quick look at distribution maps of mammals around the Baltic sea (Bjärvall & Ullström 1986) reveals that the sea presumably hinders the spread of 25% of the species. Colonisation difficulties are of course pronounced in Iceland which has a depauperate mammalian fauna, typical of oceanic islands (Brown 1989).

Young communities often have fewer species than old ones (Orians 1986) and may, therefore, be easier to invade (Moulton & Pimm 1986). On the other hand, the harsh climate of the North may pose a problem to species not physiologically fit for such conditions (Begon et al. 1990, p. 829), and therefore, it is unlikely that northern areas should be subject to large invasions in spite of their low diversity (Brown 1989).

In this article, the success rate of wildlife introductions to Nordic countries will be presented and their effects briefly described.

Successful and non-successful colonisers

Of 'game-sized' animals (cosmopolitan rats *Rattus* spp. and house mouse *Mus musculus* are not included), 10 exotic mammal species and, at least, four bird species new to the Nordic countries have successfully established populations in the wild (Table 1). An eleventh mammal, the raccoon *Procyon lotor*, is apparently gradually colonising Denmark from northern Germany (B. Jensen 1996, pers. comm.).

Of the 18 introductions of new species 14 have been successfull leading to a rather high success rate of 78% (Tables 1 and 2). This figure can be compared, for example, with North America where four out of 30 new game bird species (until 1948) have been successful (13%), and with Hawaii, where 30 out of 150 introduced bird species have been successful (20%) (Ebenhard 1988). The high success rate may at least partly be due to more individuals having been involved in Nordic introductions. The high success rate of introductions in the Nordic countries resembles that of Ireland and New Foundland which were cut off by the rising sea level soon after the last glaciation, when they had only ice and tundra. All five mammalian species introduced there have become established,

Table 1. Introduced species which have established populations in the wild in the five Nordic countries. Intrastate translocations are not included. ? indicates that only stray individuals and no reproduction in the wild have been observed. * indicates that this is not a new species to the Nordic countries as a whole. Sources: Denmark (Jensen 1982, B. Jensen, pers. comm.); Finland (Nummi1988); Iceland (Lever 1985); Norway (Myrberget 1987); Sweden (Ebenhard 1988).

Species	Denmark	Finland	Norway	Sweden	Iceland	Country of origin
Mink *Mustela vison*	x	x	x	x	x	North America
Polecat *Mustela putorius*			x*			Eurasia
Raccoon dog *Nyctereutes procyonoïdes*	x?	x	x?	x		East Asia
Raccoon *Procyon lotor*	x?					North America
Wild boar *Sus scrofa*				x*		Eurasia
Fallow deer *Dama dama*	x	x	x	x		Turkey
Sika deer *Cervus nippon*	x					East Asia
White-tailed deer *Odocoileus virginianus*		x		x?		North America
Reindeer *Rangifer tarandus*					x*	Holarcticum
Musk ox *Ovibos moschatus*			x	x		North America, Greenland
Mouflon *Ovis musimon*		x				Europe
Brown hare *Lepus europaeus*				x*		Eurasia
Rabbit *Oryctolagus cuniculus*	x		x	x		Iberian peninsula
Canadian beaver *Castor canadensis*		x				North America
Muskrat *Ondatra zibethicus*		x	x?	x		North America
Barnacle goose *Branta leucopsis*		x		x		Holarcticum
Canada goose *Branta canadensis*	x	x	x	x		North America
Mute swan *Cygnus olor*	x	x	x	x		Central Asia
Pheasant *Phasianus colchicus*	x	x	x	x		East Asia

leading to a success rate of 100% (Williamson & Fitter 1996).

It has been pointed out (Erlich 1986, Moulton & Pimm 1986, Brown 1989) that successful invaders normally have wide original ranges, and this also seems to be the case for many of the newcomers to Fennoscandia. The American mink *Mustela vison*, white-tailed deer *Odocoileus virginianus*, Canadian beaver *Castor canadensis*, muskrat *Ondatra zibethicus*, Canada goose *Branta canadensis* and pheasant *Phasianus colchicus* all have continent-wide original ranges. Fallow deer *Dama dama* and rabbit *Oryctolagus cuniculus*, however, are very different: the natural range of the fallow deer is confined to Turkey, and that of rabbit to the Iberian peninsula and probably northern Africa (Lever 1985).

Typically, the successful invaders of Fennoscandia originate from areas with harsh winters, and seven of them are of North-American origin (see Table 1). In the Nordic countries the mink has been the most successful invader, although the muskrat has colonised even wider areas when considering all of Eurasia (Lever 1985). The northern climate obviously limits the distribution of temperate species: rabbit, sika deer *Sika nippon*, fallow deer and pheasant are all confined to the southern parts of Fen-

Table 2. Species that have not established populations in the wild although they have either been introduced or have escaped from captivity. # indicates that reproduction units in the wild have been reported. See Table 1 for sources.

Species	Introduced to	Country of origin
Raccoon	Norway, Sweden	North America
Red deer	Finland#	Eurasia
Chamois *Rupicapra rupicapra*	Norway	Europa
Coypu *Myocastor coypus*	Denmark#, Norway, Finland	South America
Brown hare	Norway#	Eurasia
Barnacle goose	Norway#	Holarcticum
Snow goose *Anser caerulescens*	Norway#	North America
Red-legged partridge *Alectoris rufa*	Norway	Europe
Bobwhite *Colinus virginianus*	Norway	Europe
King penguin *Aptenodyctes patagonicus*	Norway	Subantarktis

noscandia, and the fallow deer of the Finnish mainland, for example, are very dependent on winter feeding (Nummi 1988).

In some cases the climate may have prevented a species from entering the Nordic fauna altogether (see Table 2). In Denmark, South American coypus *Myocastor coypus*, which escaped from fur farms, established small populations in the wild. In the long run, however, they failed to adapt to the severe winters in Denmark (Jensen 1982). In many of the unsuccessful cases, the number of released or escaped animals was so low (less than 10, see Roughgarden 1986) that the founding of a population was a matter of chance (e.g. chamois *Rupicapra rupicapra*, snow goose *Anser caerulescens* and red-legged partridge *Alectoris rufa*, in Myrberget 1987).

It has also been stated that genetic variability would enhance the success of invaders (Erlich 1986). However, in the genetically well-studied case of successful invasion of Fennoscandia, the Canada goose, genetic variability was extremely low (Tegelström & Sjöberg 1995, Sjöberg 1996). This was also the case in the successful reintroduction of the European beaver *Castor fiber* in Sweden (Ellegren et al. 1993), and the genetic variability in Finnish beavers and white-tailed deer, which originate from stocks consisting of only a few individuals, will presumably be low as well (Nummi 1988).

Colonisers are often generalists which manage well in man-influenced habitats (Erlich 1986, Moulton & Pimm 1986, but see Simberloff 1986) where disturbance has often caused resource enhancement (Orians 1986). The generalist-concept is somewhat unclear, but for example the successful predators mink and raccoon dog *Nyctereutes procyonoïdes* clearly fit into the picture (Ebenhard 1988, Kauhala 1996). Likewise, many of the newcomers evidently have benefitted from resources provided by human activity, e.g. cultivated fields and garbage heaps. These include white-tailed deer, rabbit, and pheasant. The resource enhancement is probably best seen in the raccoon dog: in the areas to which it has spread its closest possible competitors, the red fox *Vulpes vulpes* and the badger *Meles meles*, have also grown more numerous and widened their range because of the increased influence of man (Hersteinsson & Macdonald 1992, Bevanger & Lindström 1995, Kauhala 1995).

Some of the newcomers do not seem to depend on human influence for their survival. The best example of this is the muskrat, which can do well in eutrophic lakes, but which also thrives in the vast pristine areas from northern Finland to Siberia (Artimo 1960, Lever 1985).

Ecological effects of introductions

In his exhaustive review of bird and mammal introductions Ebenhard (1988, see also Diamond & Case 1986) dealt with six ways in which colonisers could affect native biota ecologically: 1) herbivory, 2) predation, 3) competition, 4) introduction of new parasites and diseases, 5) hybridisation with native species, and 6) acting as prey for native species.

Table 3. Changes in dominance of the four most common helophytes in 54 small lakes in southern Finland over 30 years (from 1947-50 to 1976-79). The dominance is expressed as the number of lakes in which a species was dominant. The decline of *Equisetum* and *Schoenoplectus* is mainly caused by the muskrat. (Adapted from Toivonen 1980).

	Dominant during	
Species	1947-1950	1976-1979
Equisetum fluviatile	22	12
Schoenoplectus lacustris	11	3
Phragmites australis	22	29
Typha latifolia	0	10

Herbivory

In isolated islands, like New Zealand, herbivores such as red deer *Cervus elaphus*, goat *Capra hircus*, and brushtail possum *Trichosurus vulpecula* have severely depleted vegetation from forest floor to tree tops in many areas (Atkinson & Cameron 1993). Effects of that magnitude are not found in the Nordic countries, but more is happening here than is evident at first sight. The muskrat alters vegetation succession patterns profoundly (Danell 1977), and it has changed species dominance relations in small lakes: in Finland, *Phragmites* and *Typha* have increased at the expense of *Equisetum* and *Schoenoplectus* (Table 3) (Toivonen & Meriläinen 1980).

Little is known about the effects of other non-indigenous herbivores, but grazing by the rabbit and especially the mute swan *Cygnus olor* would be expected to have some effect. Mute swans may reach relatively high densities even in the barren islands of the outer archipelago (Hildén & Hario 1993) and they are known to be able to reduce the amount of aquatic vegetation (Cobb & Harlin 1980). Apart from causing agricultural damage, the 'herbivorous' Canada goose is well-known for being a nuisance in the parks and at the beaches of the USA (Conover & Chasko 1985); and the Nordic countries have already become acquainted with this problem as well.

Predation

The effect of predation is not easy to assess, if it is not as dramatic as it has been in oceanic islands (see references in Ebenhard 1988). According to Kauhala et al. (1993) the raccoon dog in Finland mainly eats small mammals,

plants and carcasses and does not seem to affect native biota strongly. But heavy predation by the raccoon dog on waterfowl nests has been reported from Estonia (Naaber 1971).

The mink has probably affected native species more than the raccoon dog (Kauhala 1996), because it has also colonised the outer archipelagos of the Baltic Sea, where no such predator has previously existed; the indigenous European mink *Mustela lutreola* of Finland apparently did not inhabit large waters (Westman 1968). There seem to be differences in the ability of seabird species to adapt to mink predation. In some areas common eider ducks *Somateria mollissima* have gradually returned to islands near the mainland, from which they disappeared during the initial colonisation by mink (Gerell 1985). In other areas eider populations have increased in spite of mink colonisation (Niemimaa & Pokki 1990). Black guillemot *Cepphus grylle* and razorbill *Alca torda*, which feed their young in crevice nests for several weeks, are more vulnerable to mink predation than eiders. Hario et al. (1986) noted a clear decline in the number of breeding black guillemots in the Finnish archipelago as a result of heavy nest predation for several successive years; in some years a considerable number of hens was killed as well (Table 4) (Hario & Komu 1979).

Competition

There are two species pairs in which the American species seems to outcompete the Eurasian species: the European and American mink, and the European and Canadian beaver. As stated earlier, the American mink has colonised all the Nordic countries (see Table 1). In Finland, the American mink apparently has hindered the recovery of the European mink - the decline of which, however, started already before the increase of the American species (Henttonen & Tolonen 1983, Maran & Henttonen 1995).

At least some degree of food competition has been suggested to exist between the European otter *Lutra lutra* and the American mink (Erlinge 1972, Clode & Macdonald 1995), but the two species seem to be able to coexist; this is no wonder since the mink coevolved with the Canadian otter *Lutra canadensis* which is ecologically very similar to the Eurasian species (Mason & Macdonald 1986). However, the mink may be excluded from the preferred habitat of the otter (Erlinge 1972, Kauhala 1996).

In Finland, the Canadian beaver now inhabits all the areas where both species were introduced (Ermala et al. 1989), and it has colonised Russian Karelia (Danilov 1995). In some places in Finland, European beavers probably died out just by chance, but in one location a population of about 12 individuals died out after the introduction of only one pair of Canadian beavers (Linnamies 1956). In contrast, Danilov (1995) reported cases where Canadian beavers disappeared after the establishment of the European species. Whatever the case, it is a great task for wildlife managers to prevent the Canadian beaver from spreading further to the east, and to the south and west in Sweden and Norway.

The possible competition between white-tailed deer and roe deer *Capreolus capreolus* has also been discussed (Nummi 1988). Both species are concentrate selectors (Hofmann 1985), and the white-tailed deer is the smallest member of the deer guild in North America, while the roe deer holds a similar position in Eurasia. The difference in size between these species which reflects their ecology is probably large enough to permit coexistence of the two species. The white-tailed deer appears to use juniper *Juniperus* sp. more as food than the roe deer (Anderson & Koivisto 1980, Helle 1980). Likewise, the greylag goose *Anser anser* and the Canada goose seem to be able to coexist and both have increased in number in the same areas at the same time (Fabricius 1983). The situation, however, becomes more complicated with the barnacle goose *Branta leucopsis* entering the Baltic sea (Forslund & Larson 1991).

Parasites and diseases

The introduction of white-tailed deer into Finland met with good luck because the meningeal worm *Parelaphostrongylus tenuis* did not become established in Finland (Andersson et al. 1968), either because the introduced deer were not infected, or because there was no suitable intermediate host (a gastropod) for the parasite in Finland.

The case of the deer worm is a case where a species actually might be able to benefit from leaving its parasite behind; this is more likely to happen with parasites with indirect life cycles (Dobson & May 1986). Similarly,

Table 4. Effects of mink on the black guillemot population in the island of Söderskär in southern Finland during 1974-1979 (Hario & Komu 1979, M. Hario, pers. comm.).

	1974	1975	1976	1977	1978	1979
Nests destroyed	31	16	155	-	134	-
Females eaten	-	1	7	-	37	-
Number of breeding pairs	512	416	371	310	328	231

American mink has left some of its parasites behind (A. Tolonen, pers. comm.).

Hybridisation

Hybridisation with indigenous, related species or subspecies is not known to have strongly affected Nordic wildlife species. In Norway, however, the endemic subspecies of the red deer *Cervus elaphus atlanticus* is highly valued, and therefore, import of red deer to Norway is prohibited (Barikmo & Jaren 1988). Similarly, it has not been wise to bring Swedish wild boars *Sus scrofa* to Finland because they may have hybridised with domesticated pigs in farms.

Prey for native species

Invaders which may be prey for native species do normally not pose a big problem. In Finland, however, it has been noted that a dense pheasant population may make it difficult to reintroduce partridges *Perdix perdix* to the same area, because the pheasants sustain a dense population of goshawks *Accipiter gentilis* (Bisi 1990).

Conclusions

Introduced wildlife has been very successful in the Nordic countries. This may partly be explained by the relatively young age of the northern communities, which are associated with geographical distribution barriers. However, it must be kept in mind that many of the newcomers (e.g. muskrat, raccoon dog, Canada goose) have been successful in many different kinds of areas. Although the impacts of the introductions of birds and mammals to the Nordic countries mostly have not been very dramatic, there are two exceptions: the suspected displacement of the European mink and beaver by the American species. Additionally, the American mink has caused a new kind of predation pressure on bird colonies in the coastal areas of the Nordic countries. Of herbivores, the muskrat has been shown to affect patterns of plant abundance. The effects of other herbivores such as the mute swan still remain to be revealed.

Because animals do not respect borders, at least the Nordic countries should follow the policy regarding exotic species proposed by Ruesink et al. (1995): "guilty until proven innocent". A risk-benefit analysis should also include farmed animals which potentially may establish populations in the wild.

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