

- Herrera, E. A. & Macdonald, D. W. (1993). Aggression, dominance, and mating success among capybara males (*Hydrochoerus hydrochaeris*). *Behav. Ecol* **4**: 114–119.
- Hoefs, M. & Nowlan, U. (1994). Distorted sex ratios in young ungulates: the role of nutrition. *J. Mammal.* **75**: 631–636.
- Humboldt, F. H. A. von & Bonpland, H. J. A. (1805–37). *Voyages aux régions équinoxiales du nouveau continent . . . etc.* Imprimerie J. Smith, Paris.
- Kozłowski, J. & Stearns, S. C. (1989). Hypotheses for the production of excess zygotes: models of bet-hedging and selective abortion. *Evolution* **43**: 1369–1377.
- Leirs, H., Verhagen, R. & Verheyen, W. (1994). The basis of reproductive seasonality in *Mastomys* rats (Rodentia: Muridae) in Tanzania. *J. trop. Ecol.* **10**: 55–66.
- Loeb, S. C. & Schwab, R. G. (1987). Estimation of litter size in small mammals: bias due to chronology of embryo resorption. *J. Mammal.* **68**: 671–675.
- López Barbella, S. (1987). Consideraciones generales sobre la gestación del chigüire, (*Hydrochoerus hydrochaeris*). *Acta cient. venez.* **38**: 84–89.
- Macdonald, D. W. (1981). Dwindling resources and the social behaviour of capybaras (*Hydrochoerus hydrochaeris*) (Mammalia). *J. Zool., Lond.* **194**: 371–391.
- May, R. M. & Rubenstein, D. I. (1984). Reproductive strategies. In *Reproduction in mammals 4: reproductive fitness* (2nd edn): 1–23. (Eds Austin, C. R. & Short, R. V.). Cambridge University Press, Cambridge.
- Oftedal, O. T. (1984a). Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp. zool. Soc. Lond.* No. 51: 33–85.
- Oftedal, O. T. (1984b). Body size and reproductive strategy as correlates of milk energy output in lactating mammals. *Acta zool. fenn.* **171**: 183–186.
- Ojasti, J. (1973). *Estudio biológico del chigüire o capibara*. FONAIAP, Caracas.
- Ojasti, J. (1978). *The Relation Between Population and Production in Capybaras*. PhD thesis: University of Georgia, Athens, Georgia, USA.
- Ojasti, J. (1991). Human exploitation of capybara. In: *Neotropical wildlife use and conservation*: 236–252. (Eds Robinson, J. G. & Redford, K. H.). University of Chicago Press, Chicago & London.
- Parra, R., Escobar, A. & González-Jiménez, E. (1978). El chigüire: su potencial biológico y su cría en confinamiento. In *Informe Anual IPA*: 83–94. Universidad Central de Venezuela, Maracay, Venezuela.
- Perrin, R. & Allen-Rowlandson, T. S. (1995). The reproductive biology of the greater kudu, *Tragelaphus strepsiceros*. *Z. Säugetierk.* **60**: 65–72.
- Ramía, M. (1972). Cambios en las sabanas del Hato El Frío producidos por diques. *Bol. Soc. venez. cienc. nat.* **30**: 57–90.
- Roberts, C. M. & Perry, J. S. (1974). Hystricomorph embryology. *Symp. zool. Soc. Lond.* No. 34: 333–360.
- Samson, C. & Huot, J. (1995). Reproductive biology of female black bears in relation to body mass in early winter. *J. Mammal.* **76**: 68–77.
- Trivers, R. L. & Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**: 90–92.
- Weir, B. J. (1974). Reproductive characteristics of hystricomorph rodents. *Symp. zool. Soc. Lond.* No. 34: 265–301.
- Wright, D. D., Ryser, J. T. & Kiltie, R. A. (1995). First cohort advantage hypothesis: a new twist on facultative sex ratio adjustment. *Am. Nat.* **145**: 133–145.
- Zara, J. L. (1973). Breeding and husbandry of the capybara *Hydrochoerus hydrochaeris* at Evansville Zoo. *Int. Zoo Yb.* **13**: 137–145.

The continuing decline of the European mink *Mustela lutreola*: evidence for the intraguild aggression hypothesis

T. Maran, D. W. Macdonald, H. Kruuk, V. Sidorovich and V. V. Rozhnov

Introduction

European mink, *Mustela lutreola* (Linnaeus 1761) look so similar to American mink, *Mustela vison* (Schreber, 1777) that the two were formerly distinguished only as subspecies (Ognev, 1931; Heptner *et al.*, 1967; for a review, see Novikov, 1939). This similarity offers not only a striking instance of convergence, but also a plausible explanation of the European mink's precipitous decline to the verge of extinction. In fact, phylogenetically the European mink is probably closest to the Siberian polecat, *Mustela sibirica* (Pallas, 1773), whilst the American mink is the most aberrant in the genus *Mustela* (Lushnikova *et al.*, 1989; Graphodatsky *et al.*, 1976; Youngman, 1982).

The European mink was formerly widespread in eastern Europe, but has declined over a long period and by 1990 was clearly endangered (Maran, 1994b). Here, after reviewing briefly the species' biology, we will present the results of an up-dated survey of the European mink's status. Against that background we will present a critical review of hypotheses that might explain its decline, dwelling in particular on two that we will subject to a preliminary test by presenting new data. These two implicate the American mink, first through the transmission of disease and second as a direct aggressor. Concerning the possibility that direct aggression between the endemic and alien mink disadvantages the native species, we have in mind that intraguild competition between the two must be evaluated in the context of the entire guild. Therefore, when, elsewhere, we present data on the possibility of competition for food between these congeners, we do so in the context also of the diets of European polecat (*Mustela putorius*) and otter (*Lutra lutra*) (see Chapter 11).

The European mink, of which six subspecies have been distinguished (Novikov, 1939; Heptner *et al.*, 1967), but not universally accepted (Ognev, 1931; Youngman, 1982), is an inconspicuous denizen of small, undisturbed water-courses with rapid currents and lush riparian vegetation, in forested areas (Novikov, 1939; Danilov & Tumanov, 1976a,b; Sidorovich *et al.*, 1995). Their prey includes fish, amphibians, small mammals and invertebrates (see

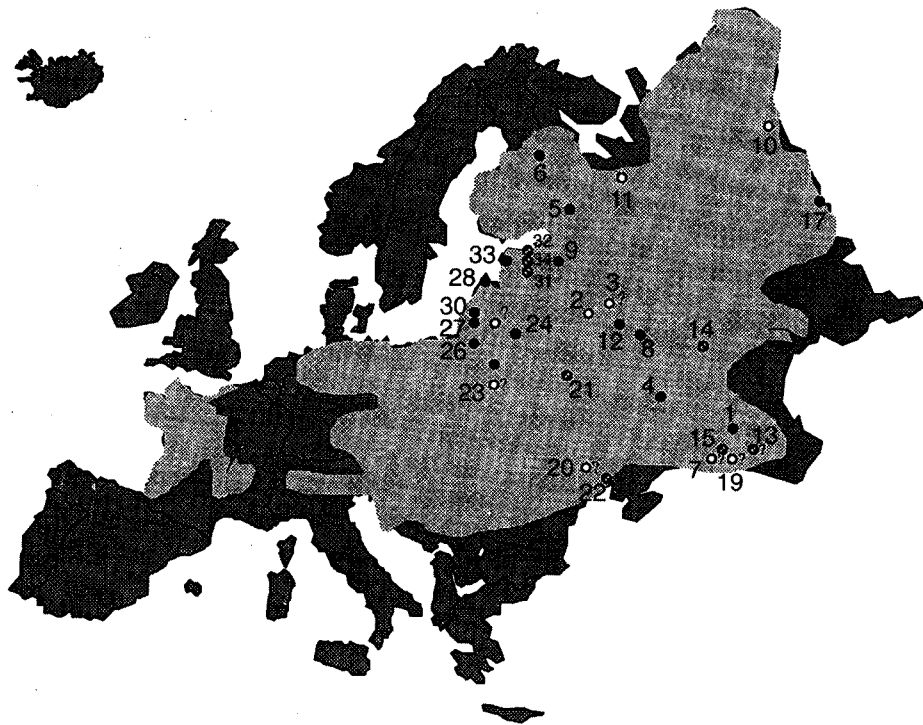


Figure 17.1. Historical and recent range of the European mink. Numbers refer to locations names in Table 17.1. ○, present 1990, present 1995; ⊙, present 1990, extinct 1995; ●, extinct in 1990; ○?, present 1990, no data 1995; ⊖, no data 1990, extinct 1995.

chapter 11, and see Danilov & Tumanov, 1976a,b; Sidorovich, 1992). European mink mate in the last 2 weeks of April, and a 43 day gestation leads, without delayed implantation, to the birth of 1–7 (mean 3.5) kits. The longest recorded lifespan for the European mink is 7 years (Maran, 1994a).

The only prehistoric records of European mink are from Vlaardingen, in the Netherlands, between 2300 and 2100 BC (van Bree, 1961a,b). From historical records the species' range once extended from the Ural Mountains to eastern Spain and from central Finland to the Black Sea (Novikov, 1939; Heptner *et al.*, 1967) (Fig. 17.1). However since the mid-nineteenth century its range has dwindled (Maran & Henttonen, 1995) and it was recently included as endangered in the IUCN Red Data Book (Groombridge, 1993). In the European Union the European mink is listed in Annex II (species whose conservation requires the designation of special areas) and in Annex IV (species of community interest in need of strict protection) of the Directive on the conservation of

natural habitats and of wild fauna and flora. The IUCN *Action Plan for the Conservation of Mustelids and Viverrids* (Schreiber *et al.*, 1989) nominates the European mink as a priority.

Course of the decline

The European Mink disappeared from Germany in the mid-nineteenth century (Youngman, 1982), then from Switzerland (Gautschi, 1983) and, in the 1890s, from Austria (Novikov, 1939). Subsequently, in western Europe, an isolated enclave of European mink originally persisted between Brittany in France and Galicia in Spain (Blas Aritio, 1970; Chanudet & Saint-Girons, 1981; Braun, 1990; Camby, 1990; Palomares, 1991; Ruiz-Olmo & Palazón, 1991). However, recently they have disappeared from the northern part of this range and appear in widespread decline in what remains of their French range (C. Maizaret, personal communication; Moutou, 1994). In intriguing contrast, and although no data exist prior to 1951, European mink are reported to be spreading southwards in Spain (Ruiz-Olmo & Palazón, 1990).

In eastern Europe the European mink's situation is almost unremittingly bad. Between the 1930s and 1950s European mink disappeared from Poland, Hungary, the Czech and Slovak Republics and probably also Bulgaria (Bartá, 1956; Szunyoghy, 1974; Schreiber *et al.*, 1989; Romanowski, 1990). In the closing years of the twentieth century, the species teeters on, or over, the brink of extinction throughout most of the remainder of its range. In Finland, following a rapid decline between 1920 and 1950 only isolated specimens were seen until the early 1970s, when the species was judged extinct until one was trapped in 1992 (Henttonen *et al.*, 1991; Henttonen, 1992). In Latvia the only evidence for the species' survival is single specimens caught in 1984, 1991 and 1993 (Ozolins & Pilats, 1995). In Lithuania, where the last record is 1979 (Bluzma, 1990), an intensive search for European mink in 1989–1990 revealed none (Mickevicius & Baranauskas, 1992). If the European mink survives at all in Georgia, it is as an extreme rarity in the rivers flowing to the Black Sea in the north-west of Georgia, where it was common in the early twentieth century (A. N. Kudatkin, personal communication; Novikov, 1939). Following a decline in Moldova in the 1930s, by the early 1980s the species survived only on the lower reaches of the river Prut, along the Romanian border (Muntjanu cited in Maran, 1994b) where it has not been seen for 15 years and is now considered extinct (A. Mihhailenko, personal communication). In Romania itself, where European mink are legal game, as recently as 1970 2700 pelts were recorded by state hunting organizations. Subsequently, the species has plummeted to rarity in northern Romania, but is apparently more numerous but declining in the Danube delta (H. Almasan, D. Muriaru & O. Ionescu, personal

communications). Although none have been seen in Estonia since 1992, unconfirmed sightings, and the capture of an apparent hybrid with a polecat in both 1994 and 1995, suggest that remnants may persist, as they may in the Ukrainian Carpathians (Turjanin, 1986) following a major decline in the late 1950s (Tumanov, 1992). By 1990 an estimated 100–150 European mink survived in the north-east of Belarus (Sidorovich, 1992). In the early decades of this century the European mink was a common and widespread carnivore almost everywhere in western Russia where it was a valuable furbearer (Novikov, 1939). Its decline there was first noticed in the 1950s and widely lamented by the 1970s (Ternovskij & Tumanov, 1973; Ternovskij 1975; Tumanov & Ternovskij, 1975; Danilov & Tumanov, 1976a). A survey by Tumanov & Zverjev (1986) revealed that by the mid-1980s European mink had declined dramatically throughout Russia, but in the Tver regions there were still reports of 4–6 European mink/10 km of river bank. Several recent reports indicate that the European mink decline is continuing in Russia and recent reports are gloomy (Sidorovich & Kozhulin, 1994; Sidorovich *et al.*, 1995).

To conclude this litany of disaster, Maran (1992a) reported the answers to questionnaires distributed in 33 areas of the former Soviet Union, of which 16 reported extinction, 13 reported very critical status and only 4 considered the populations viable.

Summarizing the population trend, there has been a steady, long-term decline of the European Mink since the nineteenth century, which has led to the general extinction of the species in western Europe, except in Spain. This decline has accelerated very rapidly in the last three decades in eastern Europe.

Below, we present the results of a new survey.

Causes of the decline

The precipitate decline of the European mink caught conservation biologists unawares, and it was not until 1995 that Maran & Henttonen published the first synthesis of possible explanations. Here, before presenting preliminary data on two of them, we review five hypotheses, namely that the decline is caused by:

- 1 Habitat loss.
- 2 Pollution.
- 3 Overhunting.
- 4 Impact of the European polecat.
- 5 Impact of the American mink.

Habitat loss

The decline of the European mink has repeatedly been attributed to habitat loss. For example, Claudius (1866) stated that over one decade the European mink was exterminated from several districts of Germany by changes in land-use, and Löwis (1899) foresaw the rapid decline of the species in Lithuania in the wake of agricultural intensification. In the Ukraine and Moldova, Tumanov (1992) links the demise of the European mink with drainage, cultivation and land reclamation. Having evaluated competing hypotheses, Schubnikova, (1982) concluded that in at least several regions of Russia the European mink's decline was due to habitat degradation and loss, particularly in central Russia (Jaroslav, Vladimir, Ivanovo and Kostroma Regions) (see also Shashkov, 1977).

It is indisputable that urbanization and agricultural intensification have radically altered much of the post-war European landscape, generally to the detriment of wildlife (e.g. Macdonald & Smith, 1991). This is true for at least many areas in which European mink have declined and, in particular, natural riverbasins have been canalized. For example, in Estonia during the 1950s and 1960s almost half of all the wetlands were drained (Kask, 1970) and agricultural improvement affected at least 20% of the country (Mäemets, 1972). Furthermore, as European mink thrive in natural river systems (Novikov, 1939, 1970; Danilov & Tumanov, 1976b) and especially in undisturbed streams (Novikov, 1939, 1970; Sidorovich *et al.*, 1995), it seems obvious that these twentieth century landscape changes will have been to their detriment. Nonetheless, beyond this loose historical correlative evidence, there have been no direct quantitative tests of the hypothesis that habitat loss caused their decline. Moreover, while there are sites, perhaps many, where radical degradation of habitat would seem to render rivers inhospitable for the mink, there are other places where the species has declined in apparently suitable habitat. Furthermore, in areas where the European mink is still present, its choice of habitat appears to include types of vegetation and banks that are still in abundance in areas where the species has gone. Therefore, to test this hypothesis rigorously, data are needed to elucidate which aspects of landscape change are detrimental to European mink.

Pollution

Pollution has been mooted as contributing to the European mink's decline by Schröpfer & Paliocha (1989). Riparian pollution is locally severe in Europe, including some areas where European mink do, or did, occur (Blas Aritio, 1970; Novikov, 1970). Furthermore, López-Martin *et al.* (1994) report organochlorine residues in European mink at levels that could perhaps impair

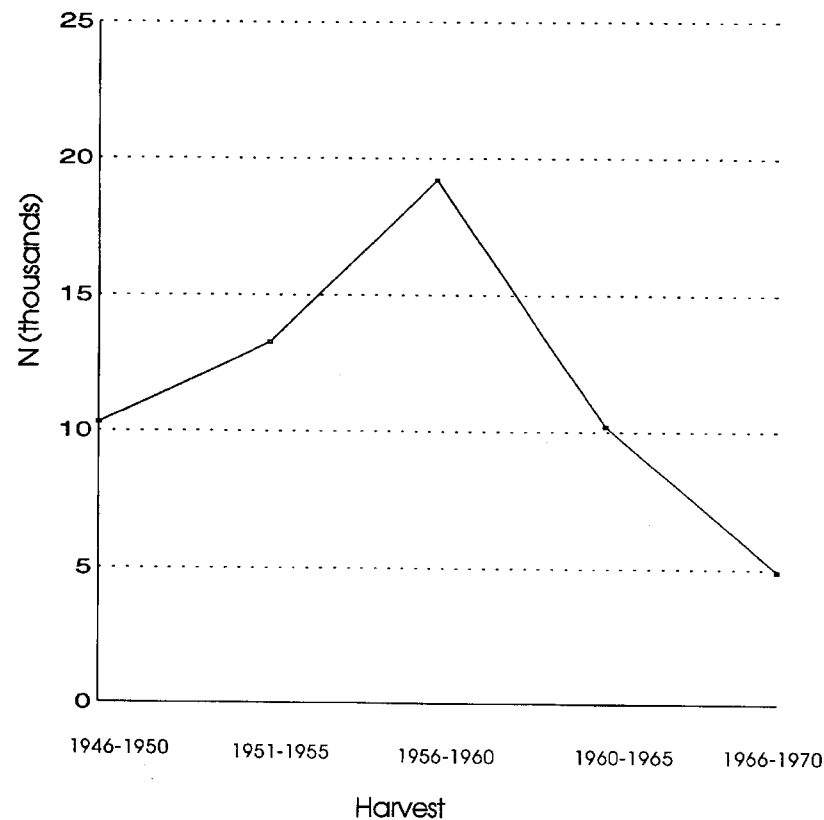


Figure 17.2. Harvest of mink in central regions of Russia (after Shashkov, 1977)

reproduction, although this report is from an area of Spain where the species is doing well. However, while this hypothesis remains largely untested, European mink have declined in some wilderness areas (such as north-eastern Belarus: see Chapter 11) which do not appear to be gravely polluted.

Overhunting

At least in the eastern part of its range the European mink has traditionally been trapped for its pelt. For instance, Schubnikova (1982) reports that as early as the seventeenth century 11 500 mink pelts were exported annually from the Arkhangelsk Region of Russia alone, while in the early decades of the twentieth century the annual Russian bag was 40 000–60 000 with a maximum of 75 000 in the winter of 1927–28. Overhunting was perceived as such a threat to the fur harvest that a moratorium on killing European mink was imposed around the

former Leningrad and in the north Caucasus at the beginning of the present century (Novikov, 1939). Following World War II, intensive harvest of European mink continued apace in Russia and, after 15 years of increasing tallies, plummeted – a decline that Shashkov (1977) attributed to local extinctions due to overhunting (Fig. 17.2).

Scarcity appears to have affected the demand, and thus value, of European mink pelts. In the late nineteenth century in Russia the pelts of European mink and polecat were valued equally (Martenson, 1905) whereas by 1983 in the Soviet Union the value of an unspecified mixture of the two mink species had increased tenfold in real terms and fetched twice the price of polecats (Maran, 1991). Although it is difficult to separate the inflationary effects of fashion and scarcity, the end result is an increased incentive to trap European mink. The official harvest target in the 1960s and 1970s in the Jaroslav Region was 28–35% of the estimated total European mink population prior to the hunting season, and approximated the annual productivity of the species (Shashkov, 1977). However, Shashkov (1977) shows that, at least for the Kostroma Region, the actual harvest was double the official figure.

Clearly, prolonged, widespread hunting significantly in excess of a population's recruitment will inevitably lead to its decline. Hunting statistics provide compelling, if somewhat fragmentary, evidence that European mink have been seriously over-harvested in some regions. This is the first of several instances in which the spread of American mink in Europe both complicates the interpretation of data and may disadvantage the European mink. First, the hunting statistics for European mink may be confounded by confusion between the two species. Second, the expanding population of American mink may have sustained the incentive for trapping beyond the time at which numbers of European mink were so low that they alone were not economically harvestable. However, although over-hunting has clearly been rife, and continues to be so (Sidorovich *et al.*, 1995), and although it seems certain to have reduced their numbers in many places, there is no clear evidence that it has been the sole, or principal, cause of European mink disappearance anywhere. Indeed, on the grounds that other semi-aquatic mustelids, such as American mink, polecat and otter, have not been exterminated by comparably intense hunting, support for this hypothesis requires evidence that European mink are strongly selected by hunters or very much more susceptible to hunting pressure than are their congeners.

Impact of the European polecat, *Mustela putorius*

In a variant of the habitat-change hypothesis, Schröpfer & Palioccha (1989) argue that landscape changes associated with agricultural encroachment have

