Biological Conservation 143 (2010) 1355–1363

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Multiple introductions determine the genetic structure of an invasive species population: American mink *Neovison vison* in Poland

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ARTICLE INFO

Article history:
Received 4 September 2009
Received in revised form 4 March 2010
Accepted 9 March 2010
Available online 13 April 2010

Keywords:
Invasive alien species
Multiple introductions
Gene flow
Propagule pressure
Mink farming

ABSTRACT

Genetic diversity of feral and ranch American mink was studied in order to understand the processes of invasion and the possible influence of multiple introductions on the feral mink population in Poland. Tissue samples obtained from feral mink taken from 10 sites across Poland (196) and from ranch mink at nine mink farms (147) were genotyped at 14 microsatellite loci. Genetic differentiation among the separate regions and sites indicated some restriction in gene flow among them (pairwise F_{ST} values), and greater variation at microsatellite loci for feral mink was attributed to differences among sites rather than among regions (AMOVA). A Mantel test demonstrated a positive association of pairwise genetic and geographic distances. A total of five clusters of feral mink were identified and their spatial distribution partially reflected regional distribution, but also suggested that there were other factors (human-mediated propagule pressure) shaping mink genetic structure. Feral and ranch mink belong to two genetically separate clusters and an assignment test showed that 34 feral mink (17%) were assigned to the ranch mink clusters. The proportion of feral mink assigned to ranch mink clusters correlated with the size of the farm breeding stocks in the districts where sampling sites were located. High human-mediated propagule pressure (particularly in western Poland) increases feral population genetic diversity and overwhelms genetic structure and potential management units, making the control of mink populations less successful. Our results indicate that reducing number of escapees from farms should be required management action.

1. Introduction

The introduction of exotic species can potentially pose a serious threat to native fauna and often leads to a dramatic loss of biological diversity (Vitousek et al., 1996), especially when the alien species increase their abundance massively, become invasive and expand their range rapidly (e.g. Brzeziński and Marzec, 2003; Arim et al., 2006). Colonization of a new area may result from single or multiple introductions of individuals (Dlugosch and Parker, 2008), but if the number of founders is small, genetic bottlenecks and genetic drift are observed. Therefore, genetic diversity is expected to decline across the expanding range of an exotic species (Allendorf and Lundquist, 2003; Rollins et al., 2009). Low genetic diversity of introduced species may reduce the colonization rate by decreasing the ability to adapt to the novel non-native environment (Falconer and Mackay, 1996; Spielman et al., 2004). Furthermore, colonization of a heterogeneous landscape with habitats of various permeabilities may accelerate genetic structuring across an invasive species' range. Such a structured range, separated by distance and/or barriers, creates units where, in separate localities, population dynamics may differ in response to variation of environmental conditions or human impact.

Theoretically, models of species invasion may be complicated by multiple introductions beyond invasion range or at locations already colonized. Multiple introductions increase genetic diversity and homogenize genetic structure across the species range (Dlugosch and Parker, 2008). A large number of propagule introduction events may increase the invasion rate by multiplying the number of animals, affecting population dynamics and compensating for the negative influence of environmental factors or human impact. Moreover, the increase in genetic diversity, which frequently leads to greater adaptability and life history plasticity (Facon et al., 2008), may further enhance a species' ability to invade. Therefore, mitigation of ongoing invasion and management of alien species require information about the colonization history, population structuring and propagule pressure. Analysis of the genetic variability and genetic structure of invasive species in a new range

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doi:10.1016/j.biocon.2010.03.009

can provide much of this important information: defining management units, landscape barriers and pathways of introduction (Rollins et al., 2009), which may greatly benefit the management strategy and improve local on-the-ground control or eradication programmes.

In the 20th century, the rapid expansion of feral American mink (*Neovison vison*) occurred in many European countries (Gerell, 1967; Cuthbert, 1973; Bevanger and Henriksen, 1995; Kauhala, 1996; Brzeziński and Marzec, 2003) and numerous stable populations are now present over a wide geographic range, comprising the whole continent (see review by Bonesi and Palazon, 2007). Since the start of the American mink invasion, fur farms have remained the predominant source of new generations of mink escapees, which supplement feral populations. In some regions, such as in Denmark where mink farming is highly developed, process of ranch mink inflow to feral population is still very intensive (Hammershoj et al., 2005). However, opinions differ as to the impact of escaping ranch mink on wild living populations. In Canada, escapees from farms may be responsible for declines in wild populations of the native mink, probably due to introgressive hybridization and diseases (Bowman et al., 2007; Kidd et al., 2009). Theoretical models suggest that a permanent inflow of ranch mink decreases the fitness of feral populations and may lead to population decline (Hammershoj et al., 2006); however, this theory has yet to be verified in any region of Europe inhabited by feral mink. On the other hand, due to the considerable variety of breeds kept at various mink farms over almost 100 years, the constant admixture between different genetic pools may have led to an increase in the adaptive potential of feral mink. It might be expected that in habitats with large numbers of farm escapees, increased competition between first generation immigrants leads to a low survival rate and so only individuals with the best adaptive potential breed within the existing feral population. Therefore, the genetic and ecological consequences of ranch mink escapes might be significant.

In Europe, the number of mink kept at farms is still high (Bonesi and Palazon, 2007), however, for fear of supplementing feral populations, mink farming has been drastically reduced or even banned in several countries since the 1970s (Cuthbert, 1973; Bonesi and Palazon, 2007; Bifolchi et al., 2010). In contrast, in Poland (due to economic and legislative reasons) the number of mink farms has significantly increased over the last decade (up to nearly 300). Thus, the Polish breeding stock is very large (over 700,000 breeding females) compared to many other European countries (Bonesi and Palazon, 2007). Moreover, the distribution of mink farms in Poland is very uneven, and the number of mink (breeding females) farmed in three north-western districts comprises about 90% of the total Polish breeding stock (Fig. 1).

The occurrence of feral American mink in Poland started at the beginning of the 1980s. These animals were probably both free-living immigrants introduced in the former Soviet Union and escapees from Polish fur farms. The present geographic range of feral mink covers a large part of Poland and is continuous (Brzeziński and Marzec, 2003). However, the historical and recent process of colonization is not precisely documented and the available data are not sufficient to show how local populations enlarged their range, in which regions of the country expanding populations started to mix, and how farms have affected feral populations. If the colonization of Poland was carried out by individuals from Eastern Europe, the levels of population genetic diversity should be inversely related to the degree of geographic isolation. On the other hand, if the local populations originated from different ancestors, it may be expected that due to the numerous farms and many different breeds on them, the genetic characteristics of feral mink populations differ significantly and are not related to geographic distance.

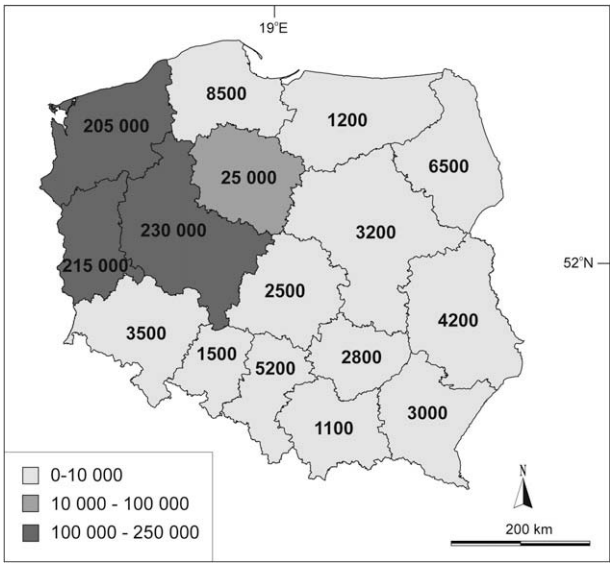

Fig. 1. Size of female breeding stocks of American mink farmed in provinces of Poland (data from the Polish Association of Fur Animal Breeders and Producers).

In many localities of its new range, American mink is considered to be particularly harmful, both as a predator and a competitor, to many native vertebrates (Woodroffe et al., 1990; Craik, 1997; Ferreras and Macdonald, 1999; Macdonald et al., 2002; Banks et al., 2008; Schüttler et al., 2009). This has led conservation organizations and authorities to suggest the extermination of feral populations, or at least the control of their numbers (Moore et al., 2003; Bonesi and Palazon, 2007; Banks et al., 2008; Ratcliffe et al., 2008). Effective control of American mink and other invasive species may largely depend on the ability to identify their introduction pathway and the connectivity between populations (Abdelkrim et al., 2005; Rollins et al., 2006, 2009; Hansen et al. 2007).

This study used molecular marker analysis to characterize genetic diversity and population structure of American mink on a large scale in order to understand the process of mink invasion and the influence of propagule pressure. The aim of the study was to answer a number of questions: (i) how current levels of genetic diversity vary among mink populations that differ with regard to the time and source of colonization, (ii) are mink populations genetically structured across the country in accordance with expectations of isolation by distance, and (iii) how extensive is gene flow between ranch and feral mink populations and how does it influence genetic structure? This information represents a first step in the development of an effective local management strategy to control American mink numbers and impact, especially in areas experiencing mink-wildlife conflicts.

2. Methods

2.1. Sampling and microsatellite genotyping

Tissue samples were obtained from feral mink trapped live by us, and from individuals killed by hunters and conservationists under legal permits during local eradication programmes in 2003–2007. Mink were sampled at 13 sites in 4 regions (NW – Northwest Poland, CE – Central Poland, SC – South Central Poland, and NE – Northeast Poland); however, at three sites located in South Central Poland (San River, middle Warta River and Milicz Ponds) no mink were captured (Supplementary material, Fig. A). Tissue samples from a total of 196 feral mink were collected at the following sites: "Warta Mouth" National Park – NW1, Gwda River – NW2, Słupia

River – NW3, Wel River – CE1, lower Narew River – CE2, middle Vistula River near Warsaw – CE3, middle Vistula River near Puławy – CE4, Mazurian Lakeland – NE1, Romincka Forest – NE2, and Biebrza National Park and surrounding area – NE3 (see Appendix A for sample sizes at each site). To compare the genetic structure of feral mink in each region with that of ranch mink, muscle tissue was also collected from 147 ranch mink from nine Polish mink farms distributed throughout the country (see Supplementary material, Fig. A and Michalska-Parda et al., 2009). In a previous description of genetic variation in ranch mink (Michalska-Parda et al., 2009) it was found that mink from the studied farms did not form distinct genetic groups, so in the present study all ranch mink were grouped in one unit. Data relating only to standard and pastel coat colour variants were used, as these types are those most often bred on farms. All tissue samples were placed in 95% ethanol and stored at −20 °C prior to DNA extraction.

DNA was extracted from tissue samples using an A&A Biotechnology DNA extraction kit, following the manufacturer's instructions. Fourteen microsatellite loci developed for mink were used to genotype individuals: Mvi87, Mvis075, Mvis020, Mvi54, Mvi586, Mvi111, Mvi219, Mvis072, Mvis099, Mvis027, Mvis192, Mvi57, Mvi232, Mvis002 (O'Connell et al., 1996; Brusgaard et al., 1998; Fleming et al., 1999). The microsatellites were amplified in three multiplex reactions prepared using a Multiplex PCR Kit (QIAGEN). Reaction mixtures contained approximately 2 μl of template DNA in a total volume of 12.5 μl. The thermal cycle, performed in a Helena BioSciences HB cycler, consisted of an initial denaturation step at 95 °C for 15 min, followed by 35 cycles of 94 °C for 30 s, 60 °C for 1 min 30 s, and 72 °C for 1 min. The amplified fragments were resolved by electrophoresis using a Beckman Coulter CEQ 8000 automated DNA sequencer and analysed using CEQ 8000 Genetic Analysis System version 9.0 software.

2.2. Genetic variability analysis

Microsatellite data were checked for departures from Hardy–Weinberg linkage equilibrium (GENEPOP 3.4; Raymond and Rousset, 1995) and the presence of null alleles (CERVUS 3.0.3; Marshall et al., 1998). Loci that consistently departed from equilibrium, showed linkage equilibrium or evidence of null alleles were removed from further analyses.

The genetic variability of each locus within the feral populations was estimated as the mean allele number (A), observed heterozygosity (H_O) and expected heterozygosity (H_E) using FSTAT (Goudet, 1995) and GenAlex version 6 (Peakall and Smouse, 2006). The mean number of alleles per locus is expected to be sensitive to sample size, and estimates of the expected allele number per locus and mink origin were corrected for unequal sample sizes (Ar). The inbreeding coefficient (F_{IS}) and potential deviation from the Hardy–Weinberg equilibrium and linkage equilibrium for each locus and site were tested using the randomization test in GENEPOP 3.4 (Raymond and Rousset, 1995). The genotypic disequilibrium test for each locus and site pair was also performed using GENEPOP 3.4 (Raymond and Rousset, 1995). Bonferroni's correction was applied to multiple comparisons.

Genetic structuring of American mink was assessed using various methods. FSTAT 2.9.3 software (Goudet, 1995; Goudet et al., 2002) was used to calculate pairwise F_{ST} estimates to summarize genetic variation between populations. For visualization of the differences based on F_{ST}, dendrograms were constructed using the program Mega 4.1 (Kumar et al., 2004). Analysis of molecular variance (AMOVA) implemented in ALREQUIN 3.1 (Excoffier et al., 2005) was used for an initial comparison of genetic structures within and among three sampling regions. Data were analyzed using regions, sites within regions and individuals within sites as sources of variance. The presence of genetic isolation-by-distance (Slatkin, 1993) was assessed by testing the correlations between genetic distance (expressed as $F_{ST}/(1 - F_{ST})$; Rousset, 1997) and the geographic distances between the ten sampling sites. Geographic distances between pairs of sites were calculated as a straight-line-distance between the central points of each site (using ArcGis 9.0). The Mantel test, performed in the Isolation by Distance Web Service (Jensen et al., 2005), with significance based on 10,000 matrix permutations, was used for this correlation analysis.

Cryptic genetic structure of American mink was assessed using STRUCTURE 2.2 software (Pritchard et al., 2000). The greatest rate of change of the likelihood function with respect to K (ΔK) was used to find the most likely K (Evanno et al., 2005). In the first round of STRUCTURE analysis, a search was performed for the number of genetically different populations using the entire data set, including feral and ranch mink. This method usually detects only the uppermost level of genetic structure (Evanno et al., 2005). As we were most interested in feral mink genetic structure, a hierarchical approach (Coulon et al., 2008) was used to detect further levels of structure. STRUCTURE analyses were subsequently applied for partitioned data to detect further levels of structure in subsets of the data. Each round of STRUCTURE analysis used the model which assumed no prior information about the population, and the admixture model with correlated allele frequency parameters ($\lambda = 1$) and a burn-in phase of 500,000 interactions followed by a run phase of 500,000 interactions. Posterior probability values for the number of populations (K), ranging from 1 to 14 in the first level of structure, 1–10 in the second and 1–6 in the third, were calculated from 10 independent runs to establish consistency. To assess the number of ranch mink in the feral population, the proportion of individuals with membership $q \geqslant 0.8$ in the first level of structure analysis was estimated.

3. Results

3.1. Microsatellite variation and linkage disequilibrium

Two loci (Mvi87 and Mvis020) showed consistent heterozygote deficiency, and possible null alleles were detected for these loci (frequency > 0.580). For the other 12 loci, the frequency of null alleles varied between 0.190 and 0.014. Furthermore, Fisher's exact test detected significant linkage disequilibrium between Mvis020 and Mvis075. Therefore, the two loci Mvi87 and Mvis020 were excluded from further analysis. With the remaining 12 loci, thirty-two of the 660 locus pairs showed deviation from genotypic equilibrium that was significant at $p < 0.05$ according to Fisher's exact test. This apparent random scattering of instances of linkage disequilibrium across locus pairs confirmed the validity of utilizing data generated using these 12 markers to assess levels of genetic diversity and structure within populations.

All 12 microsatellite loci were polymorphic and the total number of alleles per locus ranged from six (Mvis002 and Mvis027) to 15 (Mvis099), with an overall mean of 10.5 (SE ± 0.87) alleles per locus. The average number of alleles per locus within the sampling sites (Appendix A) ranged from 4.2 (NW3) to 7.3 (NE3), with a mean of 5.3 ± 0.37. All sampled sites showed intermediate values of expected heterozygosity (H_E = 0.543–0.698) and observed heterozygosity (H_O = 0.512–0.669) (Appendix A). Two of the 10 sampling sites (CE4 and NE1) showed significant deviation from Hardy–Weinberg expectations after Bonferroni correction. In both instances, this was due to a deficiency of heterozygote genotypes. Single-locus Hardy–Weinberg equilibrium tests showed that heterozygote deficits were attributable to the locus Mvis075 at the CE4 site and loci Mvi54, Mvis072 and Mvis027 at the NE1 site.

Table 1
Pairwise F_{ST} comparisons between samples taken in three regions of Poland. $^{*}p < 0.05$. $^{**}p < 0.005$. $^{***}p < 0.001$. NS, not significant. Samples size given in parentheses. See Supplementary material and the text for the names and locations of the sampling sites.

Sampling site	Northwest Poland			Central Poland				Northeast Poland		
	NW1 (32)	NW2 (9)	NW3 (11)	CE1 (11)	CE2 (13)	CE3 (8)	CE4 (27)	NE1 (34)	NE2 (8)	NE3 (43)
NW1	–	***	***	*	***	***	***	***	***	***
NW2	0.0687	–	**	NS	**	*	***	***	NS	***
NW3	0.1020	0.0781	–	**	***	**	***	***	**	***
CE1	0.0276	0.0868	0.0957	–	**	*	***	***	*	***
CE2	0.0712	0.1139	0.1503	0.0852	–	NS	***	***	***	***
CE3	0.0439	0.0962	0.1399	0.0570	0.0375	–	***	*	*	***
CE4	0.0869	0.1258	0.1717	0.1020	0.0897	0.0458	–	***	***	***
NE1	0.0687	0.0982	0.1222	0.0587	0.0786	0.0719	0.1019	–	NS	***
NE2	0.0906	0.0959	0.1461	0.0916	0.0798	0.0972	0.1334	0.0636	–	**
NE3	0.0521	0.0753	0.1143	0.0542	0.0827	0.0634	0.0773	0.0401	0.0437	–

3.2. Genetic structuring and isolation by distance among feral populations

Genetic differentiation of feral mink among regions and sites was suggested by pairwise F_{ST} values (Table 1). The F_{ST} values ranged from 0.028 to 0.172 and nearly all values were statistically significant after sequential Bonferroni correction, suggesting significant differentiation among sampling sites and indicating some restriction in gene flow between them. Exceptions were adjacent sites from Northeast (NE1 and NE2) and Central Poland (CE2 and CE3), as well as adjacent sites from separate regions (NW2 and CE1), which did not differ significantly, suggesting that some gene flow occurs between them. The greatest levels of differentiation were observed between NW3 and sites from Central and NE Poland (Table 1), despite the fact that they were not the most geographically distant sites. A neighbour-joining tree based on F_{ST} showed that genetic relationships between mink populations reflect their geographic location (Supplementary material, Fig. B). According to the results of the AMOVA, nearly 92% of the total genetic variation at microsatellite loci for feral American mink was attributed to differences among individuals within the same site (Table 2). Low but still significant genetic differentiation between sites within regions was indicated by approximately 7% of the overall variance. Only 1% of the overall variance was attributed to differences between the regions.

The results of the Mantel test showed no significant positive association of pairwise genetic distance and geographic distance ($r = 0.309$, $p = 0.082$), which after ln transformation of the geographic distance became significant ($r = 0.428$, $p = 0.014$; Fig. 2). An examination of the isolation-by-distance plot (Fig. 2) indicated that the pairwise genetic distances of the NW1 site form an outlying cloud of points that may be influencing the significance revealed by the Mantel test. Re-analysis of the data after excluding site NW1 showed very strong significant correlation between genetic and geographic distances ($r = 0.760$, $p = 0.0002$; after ln transformation of geographic distance $r = 0.760$, $p = 0.0002$).

Table 2
Results of hierarchical AMOVA comparing genetic variation of feral American mink representing 10 populations within three regions of Poland. Levels of significance are based on 1000 random permutations.

Source of variation	d.f.	Sum of squares	Fixation index	Percentage of variation	*P*-value
Among regions	2	41.729	$\Phi_{CT} = 0.013$	1.33	<0.001
Among sites within regions	7	77.546	$\Phi_{SC} = 0.069$	6.85	<0.001
Within sites	382	1204.430	$\Phi_{ST} = 0.082$	91.82	<0.001
Total	391	1323.704			

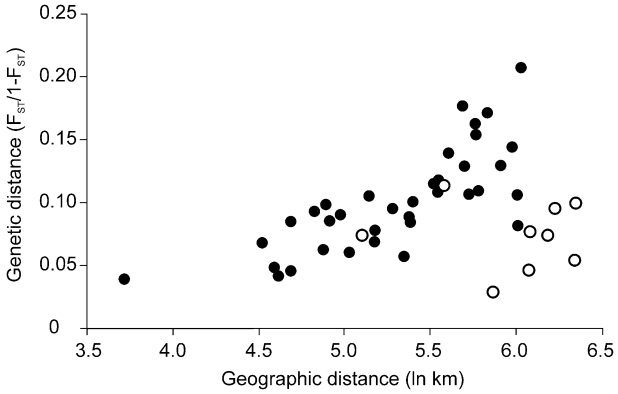

Fig. 2. Scatter plot of the Euclidean distance (natural logarithm of geographic distance – ln km) *versus* genetic distance ((FST/(1-FST); Rousset, 1997) between feral American mink sampling sites in Poland. Data points involving site NW1 are indicated by open circles.

3.3. Clustering of ranch and feral populations

The clustering approach used by STRUCTURE to determine the number of genetic groups across the entire data set of feral and ranch mink in Poland identified three hierarchical levels of subdivision. Initial partitioning of the data set indicated the presence of three clusters with the highest ΔK value (Evanno et al., 2005) (Supplementary material, Fig. C). Most individuals from sampling sites in NE Poland and CE4 were assigned to one cluster (indicated by yellow) and all ranch and feral mink individuals from sites NW1, NW2, NW3 and CE1, to two other clusters (brown and blue; Fig. 3, Fig. 4). Sites CE2 and CE3 showed evidence of admixture. A second round of STRUCTURE analysis of the feral mink subset indicated the presence of four genetic clusters. Although the $K = 4$ model did not have the absolute maximal posterior probability value, it was supported by the highest ΔK (Supplementary material, Fig. C). The first cluster (yellow) split all sites from NW Poland and site CE1, with the average proportion of membership q from 0.487 to 0.704 (Fig. 4). However, in site NW1, a higher proportion of admixed individuals was observed. The second and third clusters separated mink from the sites CE2 and CE4. Individuals from site CE3 had a mixed assignment, with two of eight assigned to the cluster 2 (blue), and six individuals to the cluster 3 (red). The fourth cluster split all sites from NE Poland with membership q ranging from 0.508 to 0.650 (Figs. 3 and 4). The third round of hierarchical analysis, identifying further clustering within the NW region, separated individuals into two other main clusters (Fig. 3). The individuals from sites NW1 and CE1 were clearly grouped into one cluster, and separated from individuals from NW2 and NW3. The average proportion of membership q to cluster 1 was 0.901

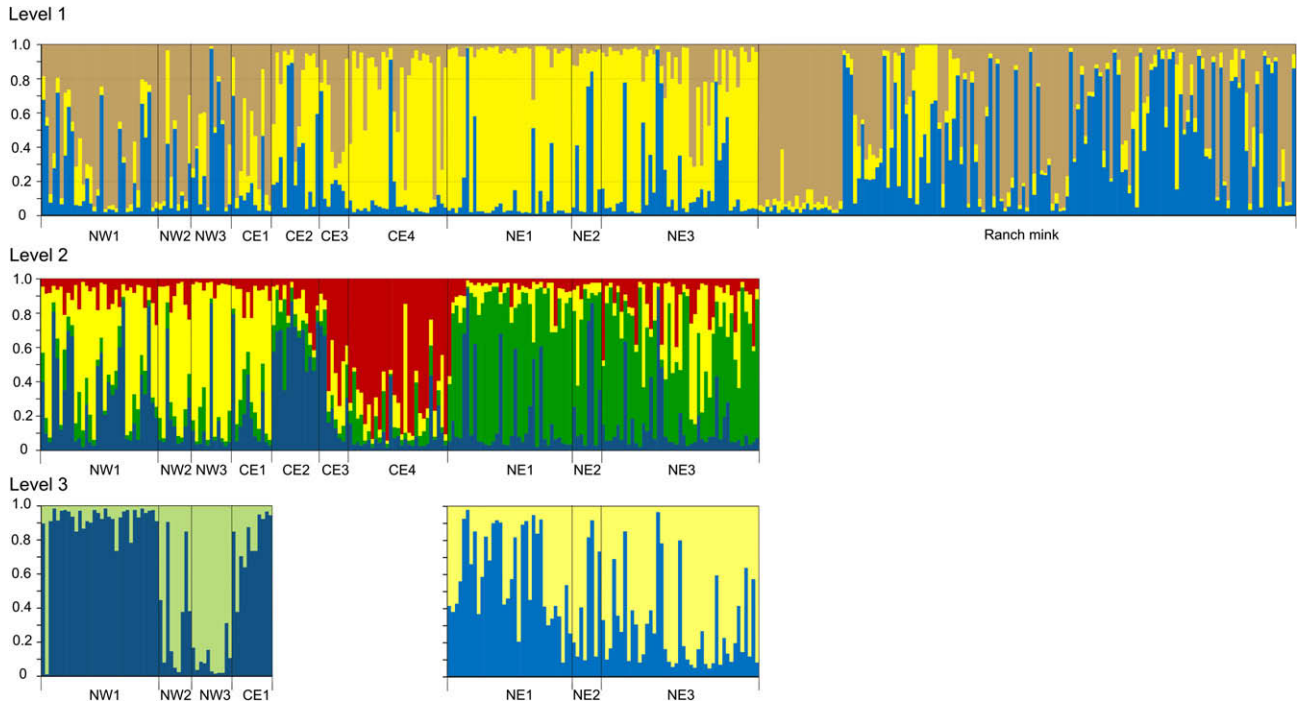

Fig. 3. Graphical output from STRUCTURE analysis representing hierarchical data analyses to determine the number of genetic groups (*K*) of American mink. Each mink is represented by a single vertical bar. The locality of origin for each individual is indicated below the plot (see the text and Supplementary material for details). At the Level 1, cluster 1 indicated by brown, cluster 2 by blue and cluster 3 by yellow; at the Level 2, cluster 1 indicated by yellow, cluster 2 by blue, cluster 3 by red and cluster 4 by green.

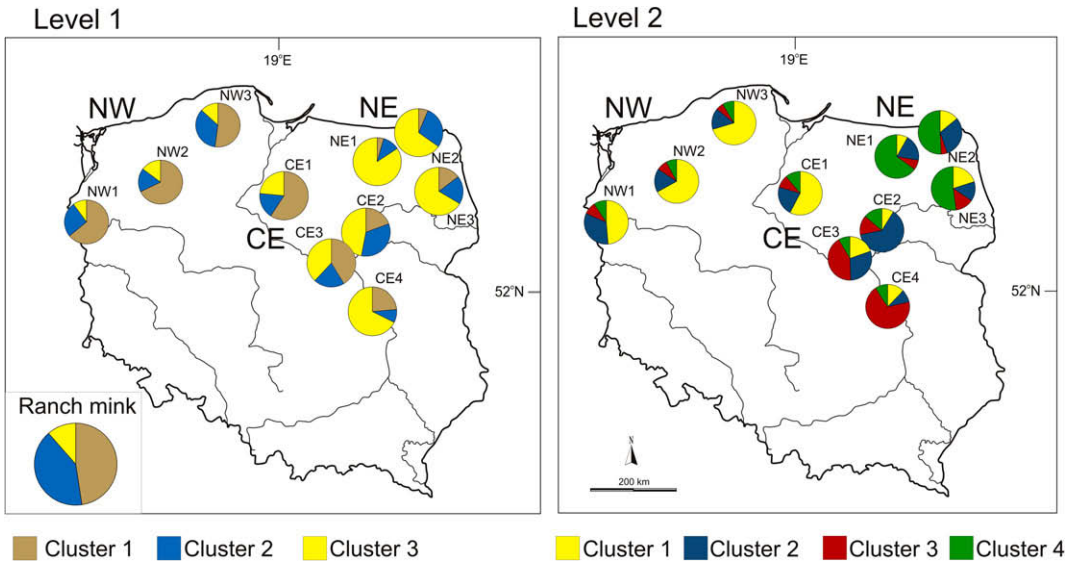

Fig. 4. The average proportion of membership for the clusters identified by STRUCTURE, representing hierarchical data analyses of feral and ranch mink in Poland. See Fig. A in the Supplementary material and the text for the locations and names of the sampling sites.

for individuals from NW1 and 0.790 for individuals from CE1; and to cluster 2 was 0.639 and 0.881 for individuals from sites NW2 and NW3, respectively. No clear partitioning of samples collected from the NE region was supported by STRUCTURE, as many individuals were strongly admixed between two clusters (the average *q* values for sites NE1, NE2 and NE3 to cluster 1 were 0.605, 0.428 and 0.281; and to cluster 2 were 0.400, 0.570 and 0.720, respectively). Following three rounds of analysis, a total of 5 clusters of feral mink and two clusters of ranch mink were identified. The spatial distribution of the five feral clusters partially reflected their distribution in regions, but also suggested that there were other factors shaping mink genetic structure, as individuals from some distant sites were grouped in one cluster (NW1 and CE1), and individuals from some neighbouring sites were assigned to separate clusters (CE2 and CE4).

Assignment tests showed that 162 mink (83%) sampled from the feral population were assigned to the feral group, whereas 34 mink (17%) from this population were assigned to the ranch mink clusters, with thresholds of $q \geqslant 0.8$. The proportion of individuals assigned to ranch mink clusters varied between regions and sites

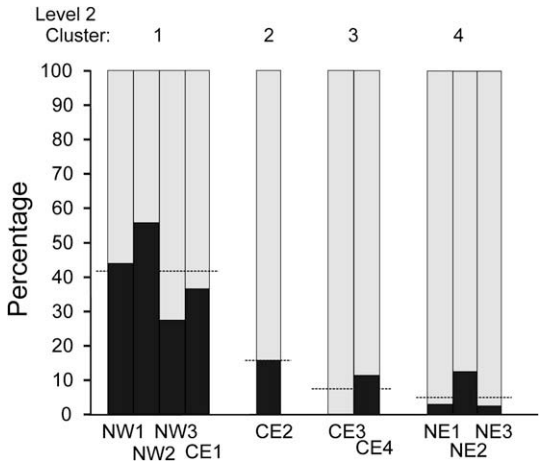

Fig. 5. Percentage of escapees from mink farms (black) for each feral mink study site, assigned using STRUCTURE with $q \geqslant 0.8$. See Fig. A in the Supplementary material and the text for locations and the names of the sampling sites; see Appendix A for sample sizes. The broken line indicates the average percentage of escapees for each cluster.

(Fig. 5). In region NW and site CE1 (Cluster 1 at the second level of STRUCTURE analysis), 41% of individuals (26/63) were assigned to the ranch mink cluster. This proportion was lower in other sites: 15% from CE2, 9% from both CE3 and CE4, and only 3% (3/85) from NE Poland. These results show a very clear gradient in the proportion of ranch mink in feral populations, which increased from east to west (Fig. 5). This gradient correlates with the distribution of mink farms in Poland (Fig. 1). The proportion of ranch mink in the feral population was significantly positively related to the female ranch mink breeding stock in each province ($R^2 = 0.64$, $n = 10$, $p = 0.005$).

4. Discussion

4.1. Genetic structure and the history of colonization

The results of genetic analyses (F_{ST} values) showed that the feral American mink population in Poland is not genetically homogenous, but is characterized by a well pronounced genetic structure. This was confirmed by the results of analyses using the STRUCTURE software, which demonstrated the occurrence of four significantly distinct genetic subpopulations. Three of them inhabit north-eastern and central Poland, and one inhabits the western and north-western part of the country. Such genetic structure was confirmed by AMOVA, which revealed that more of the genetic variance was attributable to differences among sampling sites in separate regions than to differences between regions.

In their new range, the genetic structure of invasive species is often well developed (Zeisset and Beebee, 2003; Herborg et al., 2007; Rollins et al., 2009), and sometimes invasive species exhibit higher structure than native populations (Marrs et al., 2008). In Europe, regional genetic diversity of feral American mink has also been recognized in Scotland (Zalewski et al., 2009) and Spain (Lecis et al., 2008) and was created both by geographic barriers such as mountain ranges, as well as by the distribution of farms from which the feral populations originated. In northern and central Poland there are not many landscape features (e.g. mountain ranges) that could explain the isolation of local feral mink populations. This indicates that the genetic diversity among these populations can be explained mainly by their different origin and age.

Our data suggest different colonization models for eastern and western Poland. The former was colonized by a wave of invaders from Belarus, whereas a large part of the latter was colonized by descendents of escapees from local farms. This scenario is consistent with field observations of mink colonization in Poland. The first reports on the expanding feral mink population in Poland come from the early 1980s. At that time, feral mink were observed mostly in north-eastern Poland, close to the border with Belarus (Ruprecht et al., 1983; Romanowski et al., 1984). At the beginning of the mink expansion in Poland, mink farming was poorly developed in the eastern provinces and it is likely that ranch mink escapees contributed little to the dispersing feral population. Therefore, the animals that colonized eastern Poland were migrating descendants of mink released into the wild as game animals in Russia and Belarus in the 1930s and 1950s (Ruprecht et al., 1983). Subsequently mink dispersed towards the west and south (mainly along the network of lakes in the Mazurian Lakeland and along the Vistula River and its tributaries) (Brzeziński and Marzec, 2003). A similar "stepping stone" model of mink expansion was recorded in Fennoscandia, where this mustelid extended its geographic range from the south to the north (Gerell, 1967; Bevanger and Henriksen, 1995; Kauhala, 1996). The gradual genetic differentiation of the feral mink population in eastern Poland that accompanied its expansion seems to be confirmed by the relationship between geographic and genetic distances. The sites from western Poland did not fit this pattern, suggesting that other factors have affected the establishment of mink in this region. A study of the first populations from western and central Poland in the early 1990s suggested that they were established before the arrival of the colonization wave from the east (Brzeziński and Marzec, 2003). The many mink farms that have been opened in the western provinces since the 1990s has created a potentially large number of escapees to establish feral populations in western Poland. The homogenization of genetic differences would be expected in the contact zone between these two colonization waves, but over time genetic differentiation should decrease because of the high levels of gene flow between these two populations. Similarly, a study of genetic structure in the feral mink population in Brittany (France) revealed that mink originating from three geographic regions were genetically different, but in contact areas (geographically located between three distinct genetic units), the proportion of individuals of mixed origin was 32–35% (Bifolchi et al., 2010).

4.2. Influence of multiple introductions on the feral population

In Poland, the number of mink farms and the size of breeding stocks have significantly increased in the last decade (unpublished data from the Polish Association of Fur Animal Breeders and Producers). Thus, the probability of mink escapees has also increased and the level of permanent and continuous inflow of ranch mink to feral populations seems to be high. The results of the present study show that there is an ongoing input of ranch mink to the feral population. Although the number of mink escapees from particular farms is usually unknown, the inflow of ranch mink to the feral population seems to be proportional to the number of local farms and the size of their breeding stock. We found that the number of escapees or their first generation descendants was related to the density of breeding stock in a particular area. This confirms previous observations that the number of escapees caught in the wild relates to the number of mink kept at farms in that area (Bowman et al., 2007; Bifolchi et al., 2010; Kidd et al., 2009). For example, in Denmark where the number of mink farms is very high, about 80% of feral mink individuals were found to originate from farmed animals (Hammershoj et al., 2005).

The multiple introductions affect existing feral populations in many ways. In the present study, Polish mink populations exhibited very high genetic diversity. Genetic diversity of the invasive range is usually lower than in the native range, reflecting the small

founding population and/or genetic drift (Grapputo et al., 2005; Wares et al., 2005; Herborg et al., 2007; Dlugosch and Parker, 2008). The diversity of 12 microsatellite mink loci examined in our study indicated higher polymorphism (6–15 alleles per locus) in the Polish mink population than is found in the natural range of this species (4–8 alleles per locus) (O'Connell et al., 1996; Brusgaard et al., 1998; Fleming et al., 1999; Stevens et al., 2005). Compared with studies using the same 12 loci to investigate the natural range, we also observed higher polymorphism (up to four alleles per locus more in Poland). In addition the heterozygosity in Polish feral mink (H_O = 0.643) was higher than in Canadian mink (H_O = 0.419; Belliveau et al., 1999), but was similar to that in introduced mink in Spain (H_O = 0.585; Lecis et al., 2008). Although, this gives only a rough index of genetic diversity of American mink in its native and introduced ranges, it confirms the observation that multiple introductions from various sources increase the genetic variation of invasive species (Kolbe et al., 2004; Roman and Darling, 2007; Dlugosch and Parker, 2008). Furthermore, ranch mink are derived from the process of cross-breeding of different local North American subspecies (Dunstone, 1993), which has led to higher levels of genetic variability among ranch mink than in wild living native populations (Belliveau et al., 1999). Cross-breeding of feral mink with current escapees, as well as with the descendants of those individuals previously released in Eastern Europe has resulted in genetic admixture not existing in the natural range of the species. This kind of admixture combined with the high genetic variability of ranch mink has contributed to the unusual efficiency of its expansion. Thus, the paradox of invasive species, that opposes the high evolutionary potential of the expanding species to the poor genetic variability of the small number of founders, is overwhelmed by multiple introductions of individuals from different sources (Roman and Darling, 2007).

On the other hand, as a result of domestication, ranch mink should be less well adapted to natural conditions than native individuals (Price, 1984; Gilligan and Frankham, 2003; Frankham, 2008; Wisely et al., 2008). Thus, farm escapees may import potentially maladaptive genes into the feral populations, thereby weakening them and maintaining lower levels of adaptation within these mixed populations (Bowman et al., 2007; Kidd et al., 2009). Modelling mink population numbers with this assumption (Hammershoj et al., 2005) demonstrates that the quality of feral populations would be improved if escapes from farms could be prevented. However, it may be supposed that the high number of escapees entering the feral population will increase selection pressure. The survival rate of newly escaped mink is significantly lower than that of feral mink, but if escapees manage to stay alive in nature for more than two months, their survival rate is similar to feral mink (Hammershoj, 2004). Therefore, it is likely that all poorly adapted individuals will be quickly eliminated before they can breed, and only the best adapted escapees will survive and incorporate their genes in the gene pool of the feral population. Thus, the constant intensive influx of farm escapees to feral populations could help to maintain their high genetic diversity rather than cause genetic weakness. Our results seem to confirm this notion since we did not find any signs of weakness in groups of mink trapped at sites in the western part of Poland, which are intensively supplied by farm escapees. Indeed, the mean body masses of these mink were even higher than those of the feral mink from eastern Poland (unpublished data).

Our results show that the high pressure of ongoing introductions has strongly modified the genetic structure of the feral mink population in Poland. The input of ranch mink to the feral population has led to "genetic homogenization" within the local populations in western Poland. We found a pattern where mink from distantly located sites (NW1 and CE1) were closer genetically than animals from adjacent sites (NW1 and NW2). This fact should not be assumed to reflect higher gene flow between these sites, but rather human-mediated introduction of ranch mink from a similar gene pool. Similar patterns have been observed in other invasive species of plants and animals, with high propagule pressure mediated by humans (Marrs et al., 2008; Herborg et al., 2007).

4.3. Implications for management

The threat of American mink as a very effective predator of waterfowl and semi-aquatic mammals is well recognized in Europe, including Poland (Bartoszewicz and Zalewski, 2003; Brzeziński and Marzec, 2003). Therefore, it is important that the mechanisms promoting the rapid expansion of American mink in Europe should be identified and understood. Our results show that the ongoing supply of ranch mink fugitives is not necessary to sustain the feral population. In Poland, the western and eastern mink populations are affected differently by the inflow of ranch mink escapees. This theoretically enables us to compare population processes and the invasive potential of both populations. The feral mink population in eastern Poland has existed since the 1980s, with very low admixture of new, genetically different ranch individuals. In contrast, the rapid development of mink farming in western Poland has resulted in an intensive inflow of farm escapees to the feral population and the large number of farms may contribute to an acceleration of mink expansion. However, our results do not permit estimation of the demographic impact of escaping ranch mink on feral mink populations. We were only able to describe the load of ranch mink gene input to the feral population, but these data, not supported by population studies, are not sufficient to conclude that the adaptive potential of a feral mink population supported by farm escapees (western Poland) and populations with low propagule pressure (eastern Poland), is different. We distinguished three genetic clusters in eastern and central Poland (low propagule pressure), where gene flow was partially restricted. In western and partly in central Poland (high propagule pressure), we found only one such cluster. In this region, ongoing reintroductions overwhelmed any genetic structure, creating one homogenized population, where gene flow is human-mediated. This prevents the distinction of separated populations isolated by landscape barriers reducing gene flow, and in consequence the identification of potential management units within which mink could be controlled. Thus, the potential effectiveness of local mink control programmes is probably also limited.

Complete eradication of feral mink in Europe seems unrealistic (except on isolated islands) because existing feral populations have very high reproductive potential (Sidorovich, 1993), so that even without supply from farms, they quickly rebuild their numbers after any decline. However, local control of feral populations and the reduction of their negative impact on the environment seems feasible (Bonesi and Palazon, 2007; Harrington et al., 2009). Knowledge of the genetic structure of local mink populations may help to increase the success of population control in managed areas (Hansen et al., 2007).

Though there is little evidence to support the supposed benefit of multiple introductions in promoting species persistence (Dlugosch and Parker, 2008), and some species are such good invaders that they will be able to colonize a new range even if only a very small number of individuals are introduced (Allendorf and Lundquist, 2003), this remains unproven for American mink. Although Polish feral populations exist both in regions with and without mink farming, our results indicate that reducing the number of escapees should be required management action. This action – already suggested in other areas invaded by American mink (Lecis et al., 2008) – may potentially reduce genetic variability of feral mink populations, thus decreasing the adaptive and invasive potential of this species. In general, eliminating the vector and source

responsible for introductions and expansion is an important prerequisite for developing a successful management strategy (Rollins et al., 2006; Russell et al., 2009). We assume that the development of mink farming in Poland, which has led to the inflow of ranch mink to existing feral populations, has not only had negative local environmental implications (within management units which due to ongoing reintroductions become difficult to define), but should be perceived in a larger regional or even international context. Thus, we agree with the conclusion of Bonesi and Palazon (2007) that the strategic framework to address the problem of mink expansion in Europe needs to be worked out. This seems particularly important to the new EU countries in eastern Europe, which have to find a compromise between the protection of still well preserved natural resources and the demand for economic development. The uncontrolled increase in mink farming in these countries may have serious environmental consequences and the regional policymakers should become sensitive to this problem. Studies of gene flow and genetic structure of feral mink populations have fundamental implications for understanding migration processes and for creating a successful strategy to control this invasive species. However, future genetic studies should be integrated with studies of mink population dynamics and demographic responses to eradication.

Acknowledgements

We thank A. Buczyński and M. Marzec for help with trapping mink and local farms for providing mink tissue samples for our research. We are grateful to G. Kerley and J. Gittins for English correction and useful critical comments. Trapping and handling procedures were approved by the Polish Ethical Commission for Research on Animals. This study was financed by the University of Warsaw and partly by the Ministry of Science and Higher Education (Grant no: N N304 221835). The project was supported by a Marie Curie European Reintegration Grant within the 7th European Community Framework Programme to A.Z.

Appendix A

Table A1. Genetic diversity indices of sampled American mink genotyped at 12 unlinked microsatellite loci. See Fig. A in the Supplementary material and the text for the locations and names of the sampling sites. *N*, number of analysed samples; *A*, mean number of alleles per locus (direct count); Ar, allelic richness estimated by rarefaction based on a minimum sample size of $n = 7$; H_O, observed heterozygosity; H_E, unbiased expected heterozygosity; Overall F_{IS}, inbreeding coefficient based on the average of all loci; HWE, combined *P*-value estimate for departure from Hardy–Weinberg equilibrium for all loci using Fisher's method.

Region	Site	*N*	*A*	Ar	H_O	H_E	Overall F_{IS}	HWE (*P*-value)
Northwest Poland	NW1	32	6.3	4.5	0.669	0.688	0.044	0.0353
	NW2	9	4.4	4.1	0.613	0.624	0.083	0.0354
	NW3	11	4.2	3.8	0.512	0.543	0.107	0.4339
Central Poland	CE1	11	4.5	3.9	0.605	0.626	0.084	0.3071
	CE2	13	5.3	4.7	0.655	0.698	0.102	0.2068
	CE3	8	4.3	4.2	0.582	0.622	0.131	0.0318
	CE4	27	5.1	3.9	0.519	0.614	0.174	0.0001
Northeast Poland	NE1	34	7.0	4.7	0.581	0.659	0.134	0.0001
	NE2	8	4.3	4.1	0.622	0.621	0.067	0.2401
	NE3	43	7.3	4.6	0.639	0.684	0.077	0.0295

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.03.009.

References

Abdelkrim, J., Pascal, M., Calmet, C., Samadi, S., 2005. Importance of assessing population genetic structure before eradication of invasive species: examples from insular Norway rat populations. Conservation Biology 19, 1509–1518.
Allendorf, F.W., Lundquist, L.L., 2003. Introduction: population biology, evolution, and control of invasive species. Conservation Biology 17, 24–30.
Arim, M., Abades, S.R., Neill, P.E., Lima, M., Marquet, P.A., 2006. Spread dynamics of invasive species. Proceedings of the National Academy of Sciences of the United States of America 103, 374–378.
Banks, P.B., Nordstrom, M., Ahola, M., Salo, P., Fey, K., Korpimaki, E., 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13, 3–16.
Bartoszewicz, M., Zalewski, A., 2003. American mink, *Mustela vison* diet and predation on waterfowl in the Słońsk Reserve, western Poland. Folia Zoologica 52, 225–238.
Belliveau, A.M., Farid, A., O'Connell, M., Wright, J.M., 1999. Assessment of genetic variability in captive and wild American mink (*Mustela vison*) using microsatellite markers. Canadian Journal of Animal Science 79, 7–16.
Bevanger, K., Henriksen, G., 1995. The distributional history and present status of the American mink (*Mustela vison* Schreber, 1777) in Norway. Annales Zoologici Fennici 32, 11–14.
Bifolchi, A., Picard, D., Lemaire, C., Cormier, J., Pagano, A., 2010 (Evidence of admixture between differentiated genetic pools at regional scale in an invasive carnivore). Conservation Genetics 11, 1–9.
Bonesi, L., Palazon, S., 2007. The American mink in Europe: status, impacts, and control. Biological Conservation 134, 470–483.
Bowman, J., Kidd, A.G., Gorman, R.M., Schulte-Hostedde, A.I., 2007. Assessing the potential for impacts by feral mink on wild mink in Canada. Biological Conservation 139, 12–18.
Brusgaard, K., Shukri, N., Malchenko, S.N., Lohi, O., Christensen, K., Kruse, T., 1998. Three polymorphic mink, *Mustela vison*, dinucleotide repeats. Animal Genetics 29, 153.
Brzeziński, M., Marzec, M., 2003. The origin, dispersal and distribution of the American mink *Mustela vison* in Poland. Acta Theriologica 48, 505–514.
Coulon, A., Fitzpatrick, J.W., Bowman, R., Stith, B.M., Makarewich, C.A., Stenzler, L.M., Lovette, I.J., 2008. Congruent population structure inferred from dispersal behaviour and intensive genetic surveys of the threatened Florida scrub-jay (*Aphelocoma coerulescens*). Molecular Ecology 17, 1685–1701.
Craik, C., 1997. Long-term effects of North American Mink *Mustela vison* on seabirds in western Scotland. Bird Study 44, 303–309.
Cuthbert, J.H., 1973. The origin and distribution of feral mink in Scotland. Mammal Review 3, 97–103.
Dlugosch, K.M., Parker, I.M., 2008. Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Molecular Ecology 17, 431–449.
Dunstone, N., 1993. The mink. T & AD Poyser Natural History, London.
Evanno, G., Regnaut, S., Goudet, J., 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14, 2611–2620.
Excoffier, L., Laval, G., Schneider, S., 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1, 47–50.
Facon, B., Pointier, J.P., Jarne, P., Sarda, V., David, P., 2008. High genetic variance in life-history strategies within invasive populations by way of multiple introductions. Current Biology 18, 363–367.
Falconer, D., Mackay, T., 1996. Introduction to Quantitative Genetics, fourth ed. Prentice Hall, Harlow, United Kingdom.
Ferreras, P., Macdonald, D.W., 1999. The impact of American mink *Mustela vison* on water birds in the upper Thames. Journal of Applied Ecology 36, 701–708.
Fleming, M.A., Ostrander, E.A., Cook, J.A., 1999. Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). Molecular Ecology 8, 1351–1362.
Frankham, R., 2008. Genetic adaptation to captivity in species conservation programs. Molecular Ecology 17, 325–333.
Gerell, R., 1967. Dispersal and acclimatization of the mink (*Mustela vison* Schreber) in Sweden. Viltrevy 5, 1–38.
Gilligan, D.M., Frankham, R., 2003. Dynamics of genetic adaptation to captivity. Conservation Genetics 4, 189–197.
Goudet, J., 1995. FSTAT (Version 1.2): a computer program to calculate F-statistics. Journal of Heredity 86, 485–486.
Goudet, J., Perrin, N., Waser, P., 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. Molecular Ecology 11, 1103–1114.
Grapputo, A., Boman, S., Lindstrom, L., Lyytinen, A., Mappes, J., 2005. The voyage of an invasive species across continents: genetic diversity of North American and European Colorado potato beetle populations. Molecular Ecology 14, 4207–4219.

Hammershoj, M., 2004. Population ecology of free ranging American mink *Mustela vison* in Denmark. Ph.D. Thesis, National Environmental Research Institute, Kalo, Denmark.

Hammershoj, M., Pertoldi, C., Asferg, T., Moller, T.B., Kristensen, N.B., 2005. Danish free-ranging mink populations consist mainly of farm animals: evidence from microsatellite and stable isotope analyses. Journal for Nature Conservation 13, 267–274.

Hammershoj, M., Travis, J.M.J., Stephenson, C.M., 2006. Incorporating evolutionary processes into a spatially-explicit model: exploring the consequences of mink-farm closures in Denmark. Ecography 29, 465–476.

Hansen, H., Hess, S.C., Cole, D., Banko, P.C., 2007. Using population genetic tools to develop a control strategy for feral cats (*Felis catus*) in Hawai'i. Wildlife Research 34, 587–596.

Harrington, L.A., Harrington, A.L., Moorhouse, T., Gelling, M., Bonesi, L., Macdonald, D.W., 2009. American mink control on inland rivers in southern England: an experimental test of a model strategy. Biological Conservation 142, 839–849.

Herborg, L.M., Weetman, D., Van Oosterhout, C., Hanfling, B., 2007. Genetic population structure and contemporary dispersal patterns of a recent European invader, the Chinese mitten crab, *Eriocheir sinensis*. Molecular Ecology 16, 231–242.

Jensen, J.L., Bohonak, A.J., Kelley, S.T., 2005 (Isolation by distance, web service). BMC Genetics 6.

Kauhala, K., 1996. Distributional history of the American mink (*Mustela vison*) in Finland with special reference to the trends in otter (*Lutra lutra*) populations. Annales Zoologici Fennici 33, 283–291.

Kidd, A.G., Bowman, J., Lesbarreres, D., Schulte-Hostedde, A.I., 2009. Hybridization between escaped domestic and wild American mink (*Neovison vison*). Molecular Ecology 18, 1175–1186.

Kolbe, J.J., Glor, R.E., Schettino, L.R.G., Lara, A.C., Larson, A., Losos, J.B., 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature 431, 177–181.

Kumar, S., Tamura, K., Nei, M., 2004. MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Briefings in Bioinformatics 5, 150–163.

Lecis, R., Ferrando, A., Ruiz-Olmo, I., Manas, S., Domingo-Roura, X., 2008. Population genetic structure and distribution of introduced American mink (*Mustela vison*) in Spain, based on microsatellite variation. Conservation Genetics 9, 1149–1161.

Macdonald, D.W., Sidorovich, V.E., Anisomova, E.I., Sidorovich, N.V., Johnson, P.J., 2002. The impact of American mink *Mustela vison* and European mink *Mustela lutreola* on water voles *Arvicola terrestris* in Belarus. Ecography 25, 295–302.

Marrs, R.A., Sforza, R., Hufbauer, R.A., 2008. When invasion increases population genetic structure: a study with *Centaurea diffusa*. Biological Invasions 10, 561–572.

Marshall, T.C., Slate, J., Kruuk, L.E.B., Pemberton, J.M., 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7, 639–655.

Michalska-Parda, A., Brzeziński, M., Zalewski, A., Kozakiewicz, M., 2009. Genetic variability of feral and ranch American mink *Neovison vison* in Poland. Acta Theriologica 54, 1–10.

Moore, N.P., Roy, S.S., Helyar, A., 2003. Mink (*Mustela vison*) eradication to protect ground-nesting birds in the Western Isles, Scotland, United Kingdom. New Zealand Journal of Zoology 30, 443–452.

O'Connell, M., Wright, J.M., Farid, A., 1996. Development of PCR primers for nine polymorphic American mink *Mustela vison* microsatellite loci. Molecular Ecology 5, 311–312.

Peakall, R., Smouse, P.E., 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6, 288–295.

Price, E.O., 1984. Behavioral-aspects of animal domestication. Quarterly Review of Biology 59, 1–32.

Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155, 945–959.

Ratcliffe, N., Craik, C., Helyar, A., Roy, S., Scott, M., 2008. Modelling the benefits of American Mink *Mustela vison* management options for terns in west Scotland. Ibis 150, 114–121.

Raymond, M., Rousset, F., 1995. Genepop (Version-1.2) – population-genetics software for exact tests and ecumenicism. Journal of Heredity 86, 248–249.

Rollins, L.A., Woolnough, A.P., Sherwin, W.B., 2006. Population genetic tools for pest management: a review. Wildlife Research 33, 251–261.

Rollins, L.A., Woolnough, A.P., Wilton, A.N., Sinclair, R., Sherwin, W.B., 2009. Invasive species can't cover their tracks: using microsatellites to assist management of starling (*Sturnus vulgaris*) populations in Western Australia. Molecular Ecology 18, 1560–1573.

Roman, J., Darling, J.A., 2007. Paradox lost: genetic diversity and the success of aquatic invasions. Trends in Ecology & Evolution 22, 454–464.

Romanowski, J., Kaszuba, S., Koźniewski, P., 1984. New data on the occurrence of minks (Mammalia: Mustelidae) in Poland. Przegląd Zoologiczny 28, 221–223.

Rousset, F., 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145, 1219–1228.

Ruprecht, A.L., Buchalczyk, T., Wójcik, J.M., 1983. The occurrence of minks (Mammalia: Mustelidae) in Poland. Przegląd Zoologiczny 27, 87–99.

Russell, J.C., Mackay, J.W.B., Abdelkrim, J., 2009. Insular pest control within a metapopulation context. Biological Conservation 142, 1404–1410.

Schüttler, E., Klenke, R., McGehee, S., Rozzi, R., Jax, K., 2009. Vulnerability of ground-nesting waterbirds to predation by invasive American mink in the Cape Horn Biosphere Reserve, Chile. Biological Conservation 142, 1450–1460.

Sidorovich, V.E., 1993. Reproductive plasticity of the American mink *Mustela vison* in Belarus. Acta Theriologica 38, 175–183.

Slatkin, M., 1993. Isolation by distance in equilibrium and nonequilibrium populations. Evolution 47, 264–279.

Spielman, D., Brook, B.W., Frankham, R., 2004. Most species are not driven to extinction before genetic factors impact them. Proceedings of the National Academy of Sciences of the United States of America 101, 15261–15264.

Stevens, R.T., Kennedy, M.L., Kelley, V.R., 2005. Genetic structure of American mink (*Mustela vison*) populations. Southwestern Naturalist 50, 350–355.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change. American Scientist 84, 468–478.

Wares, J., Hughes, A., Grosberg, R., 2005. Mechanisms that drive evolutionary change: insights from species introductions and invasions. In: Sax, D.F., Stachowicz, J.J., Gaines, S.D. (Eds.), Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer Associates, Sunderland, Massachusetts, pp. 229–257.

Wisely, S.M., Santymire, R.M., Livieri, T.M., Mueting, S.A., Howard, J., 2008. Genotypic and phenotypic consequences of reintroduction history in the black-footed ferret (*Mustela nigripes*). Conservation Genetics 9, 389–399.

Woodroffe, G.L., Lawton, J.H., Davidson, W.L., 1990. The impact of feral mink *Mustela vison* on water voles *Arvicola terrestris* in the North Yorkshire Moors National Park. Biological Conservation 51, 49–62.

Zalewski, A., Piertney, S.B., Zalewska, H., Lambin, X., 2009. Landscape barriers reduce gene flow in an invasive carnivore: geographical and local genetic structure of American mink in Scotland. Molecular Ecology 18, 1601–1615.

Zeisset, I., Beebee, T.J.C., 2003. Population genetics of a successful invader: the marsh frog *Rana ridibunda* in Britain. Molecular Ecology 12, 639–646.