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Reproduction and behaviour of the endangered European mink (*Mustela lutreola*) in captivity

UNIVERSITY OF TARTU
Press

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers referred to in the text by Roman numerals.

I Kiik, K., Maran, T., Nemvalts, K., Sandre, S.-L., Tammaru, T. 2017. Reproductive parameters of critically endangered European mink (*Mustela lutreola*) in captivity. Animal Reproduction Science 181: 86–92.

II Nagl, A., Kneidinger, N., Kiik, K., Lindeberg, H., Maran, T., Schwarzenberger, F. 2015. Noninvasive monitoring of female reproductive hormone metabolites in the endangered European mink (*Mustela lutreola*). Theriogenology 84: 1472–1481.

III Kiik, K., Maran, T., Nagl, A., Ashford, K., Tammaru, T. 2013. The causes of the low breeding success of European mink (*Mustela lutreola*) in captivity. Zoo Biology 32: 387–393.

IV Kiik, K., Maran, T., Kneidinger, N., Tammaru, T. 2016. Social behaviour of endangered European mink (*Mustela lutreola*) litters in captivity. Applied Animal Behaviour Science 182: 61–71.

V Haage, M., Bergvall, U. A., Maran, T., Kiik, K., Angerbjörn, A. 2013. Situation and context impacts the expression of personality: The influence of breeding season and test context. Behavioural Processes 100: 103–109.

The participation of the author in preparing the listed publications (* denotes a moderate contribution, ** a high contribution, *** the leading role)

	I	II	III	IV	V
Original idea	**	*	**	***	*
Study design	***	*	***	***	**
Data collection	**	**	**	***	**
Data analysis	***	*	***	***	*
Manuscript preparation	***	*	***	***	*

1. INTRODUCTION

Loss of biodiversity is a major concern. Some conservation measures have been notable successes, but the current level of conservation action is outweighed by the magnitude of the threat (Hoffmann et al., 2010). According to the IUCN Red List 22.2% of those mammal species assessed, are globally threatened or have become during the last few decades (IUCN 2017). The best method to improve the situation is to protect ecosystems and wild populations of species, that is, to apply *in-situ* conservation. However, this is not always possible as some threatened species have already too small, fragmented populations. Eliminating all the factors causing the decline of a species is not always achievable, or may even be impossible. For example, the last black-footed ferrets (*Mustela nigripes*) were threatened by habitat loss, overhunting, a decline in prey species and an epidemic disease (Clark, 1987). In such cases *in-situ* conservation might not be appropriate, as the results of conservation actions may take too long to yield results. The last chance to save a species from extinction may be the *ex-situ* conservation, i.e. bringing the last extant individuals into an artificial environment (Canessa et al., 2016; Snyder et al., 1996).

Unfortunately, the *ex-situ* conservation is not an easy way to save a species from extinction. This method causes the animals much stress during every phase: catching the wild specimens; transporting them to the new, artificial environment; and the management in captivity with all the new interactions with surroundings and conspecifics (Morgan and Tromborg, 2007). The *ex*-situ conservation is much more expensive compared with many other conservation activities and therefore the high cost of keeping a population in an artificial environment plays also a role in the moderate success of this method (Primack and Sher, 2016). Animals should be kept in captivity as few generations as possible, otherwise they start to adapt to the captive environment in terms of morphological (O'Regan and Kitchener, 2005) and behavioural changes, which result in the development of a domestic phenotype (Price, 1999).

Saving species in captivity has generally been more complicated and less successful than improving the natural habitat of the animals. Hence, it has been considered important that the decision to remove animals from the wild is made after a thorough investigation of the situation (Dolman et al., 2015). Conde and co-workers (2011) claim that *ex-situ* conservation programmes have had a low success rate, mainly because they have been initiated too late when only a few individuals remained. Captive breeding should therefore not be considered the last chance of saving a species from extinction, but as an important tool that should be instigated before a species faces extinction (Conde et al., 2011).

Although maintaining captive populations is generally difficult and problematic, there are several successful examples (Soorae, 2011). The most prominent are perhaps those involving the golden lion tamarin (*Leontopithecus rosalia*; Kierulff et al., 2008), Przewalski's horse (*Equus ferus przewalskii*; Xia et al., 2014) and the black-footed ferret (Clark, 1987).

The case of black-footed ferret has been an important and encouraging example for all *ex-situ* projects and especially for that on the European mink. The black-footed ferret was once common throughout West Central North America, from southern Canada to northern Mexico (Clark, 1987). The species is strongly dependent on different species of prairie dogs (*Cynomys* spp.) as prey, and these ferrets also use the burrows of this rodent as shelter and denning sites (Miller et al., 1988). At the beginning of 20th century, the number of wild black-footed ferrets decreased rapidly due to overhunting and the extermination of prairie dog colonies by humans (Biggins and Schroeder, 1988). In 1967, the black-footed ferret was listed on the U.S. Endangered Species List and in 1982 on the IUCN Red List as endangered (IUCN 2017). In 1979, the last known wild individuals died and the species was thought to be extinct. However, in 1981 an additional population was found, which consisted of approximately 100 animals. To secure the survival of the species, a captive breeding programme was established. In 1985 the wild population was decimated by an epidemic of Sylvatic Plague (*Yersinia pestis*), and the remaining individuals were captured (Reading et al., 1966). A captive population of 26 ferrets was established, 18 of them could be bred. Owing to the high degree of interrelatedness among those 18 animals, the genetic diversity corresponded to no more than the equivalent of seven founders. To preserve the genetic information of these founders, semen and ovaries were taken from these animals and stored frozen for future use. These frozen semen samples are still used to fertilize females (Howard et al., 2016). In general, keeping the captive population has been successful and to date more than 9000 black-footed ferrets have been born in captivity (Bortner, 2017; Marinari et al., 2006), and more than 4000 ferrets have been reintroduced to more than 20 locations in the United States, Canada, and Mexico. There are four self-sustaining populations, unfortunately, the number of prairie dogs is often not high, which in turn affects the success of reintroduction (Salkeld, 2017). Therefore, the re-established wild populations of black-footed ferrets remain small, fragmented, and still require intensive management (Santymire et al., 2014).

The captive breeding of black-footed ferrets was not without problems. In captivity, more than 50% of males failed to sire offspring. This negatively affects the genetic diversity of the captive population and may lead to increased incidence of deleterious traits affecting the overall viability of the population. An improper mating posture, abnormally high aggression during the mating attempt and underdeveloped testes have been identified as the main factors that induce reproductive failure in males (Wolf et al., 2000). In 2000, it was reported that reproductive failure was not related to semen quality, but in 2006–2007 the percentage of normal sperm morphology in ejaculates had decreased from 50% (in 2000) to 16%. In addition, the proportion of females that became pregnant after successful copulation declined from 70% (1987–1998) to 46% (2013). The reduced breeding success may be ascribed to inbreeding depression but also changes in diet have been discussed (Santymire et al., 2015).

There is an ongoing discussion regarding the reasons why so many carnivorous species are difficult to breed in captivity. One frequently cited reason is the large size of individual territories in the wild, which implies that the animals are adapted to covering long distances daily (Clubb and Mason, 2007; Quirke et al., 2012; Zhang et al., 2004). It is difficult to recreate similar territory sizes in captivity. In many cases, captive males show more problematic behaviour than females (Paper **IV**; MacKinnon et al., 2008; Wolf et al., 2000), which may be explained by the formers' larger home ranges (Kroshko et al., 2016; Palomares et al., 2017). Maybe this forced reduction in home range is the reason males cannot cope with small enclosures, which might be a factor in the development of abnormal behaviour primarily in the male sex (MacKinnon et al., 2008; Zhang et al., 2004; Wolf et al., 2000).

One of the most important issues in terms of keeping captive carnivores, is to provide them with suitable conditions during the breeding season. There are several examples of difficulties encountered with managing animals during the mating season, but the exact problems frequently remain unknown. For example, the Asiatic golden cat *(Catopuma temminckii)* is difficult to breed in captivity. The possible reasons of their failure to mate successfully might be socialization problems, as most individuals of this captive population have not had proper contact with conspecifics. Social isolation and a lack of early socialization with conspecifics may have affected these cats' ability to interact appropriately with each other (Olsen, 2012).

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The present thesis is focused on a critically endangered carnivore, the European mink (*Mustela lutreola*). This mustelid was once common almost all over Europe but, it has disappeared from most parts of its former range. The main causes of this drastic decline are habitat loss, overhunting, and invasion of the dominant American mink (*Neovison vison*; Maran, 2007; Maran and Henttonen, 1995). As the number of European mink decreased rapidly in the wild, a decision was made to launch a captive breeding programme to prevent their extinction (Maran et al., 2017).

Among the other mustelids, the European mink is relatively well studied. The ecological information available can be used in the planning of conservation measures. There are studies about diet (Maran et al., 1998; Põdra et al., 2013b; Sidorovich et al., 1998; Sidorovich et al., 2010), habitat preference, activity, and home range in the wild (Danilov and Tumanov, 1976; Harrington et al., 2014; Novikov, 1939 cited in Youngman, 1990; Sidorovich and Macdonald, 2001; Palomares et al., 2017). Nevertheless, information about mating behaviour, the litter period, and litter dispersal, is scarce.

To ensure a successful captive breeding programme, the aim of the present research was to study the reproductive biology of the European mink in captivity. We studied hormonal profiles and the factors that influence the reproductive success of females, mating problems, social behaviour during the litter period, and individual differences in reactions to different test stimuli. Breeding biology was described in detail, including the timing of the mating season, gestation period, litter size, and hormonal changes during the breeding season (Papers **I** and **II**). In addition, the reproductive output of females was analysed. This included the number and size of litters delivered during each female's lifetime, as well as the factors (e.g. age, weight of the mother) affecting these parameters (Paper **I**).

The main problem in successfully managing the captive population of European mink was low mating success. In our study, 67% of all studied captive born males over 2004–2010 failed to pass their genes on to succeeding generations. The problem persists, with only approximately 40% of males breeding successfully every season (**III**). This negatively affects the effective population size, which leads to a reduction in genetic diversity and inbreeding depression. First, it is most important to determine the reasons for breeding failures, as only then can one make suggestions on how to improve the situation. For this reason, we conducted a detailed study of all mating attempts. We analysed which male and female traits are the main determinants of mating success. The origin of the animal, its gender, age, the identity of its partner, and the number of mating attempts in a single year were recorded (**III**).

The environment of young can have an important effect on their future behaviour (Bautista et al., 2010; Crews et al., 2009; Rödel and von Holst, 2009). In a study of American mink, it was found that the amount of time spent on social play may affect the development of adulthood social behaviour, and thereby future mating behaviour (Ahloy Dallaire and Mason, 2017). This may also be the case with the European mink. Therefore, the litter period of the European mink was a special focus to find any indications of future normal/abnormal mating behaviour. The aim was to describe the social play behaviour of European mink cubs in detail and compare it with related species. We aimed to find clues to any behavioural distortion in the captive population. Also, a more general classification of the behavioural acts of the cubs (non-contact play, duration of bites, and solitary behaviour) during the litter period was recorded. In addition, mothers' play with their cubs and aggressive behaviour of the mother was monitored and its temporal dynamics analysed (**IV**).

As do humans, other species can show individual variation in behaviour (Gosling, 2001; Sih et al., 2004). Also individuals of an endangered species may vary in how fast and successfully they adapt to a novel environment, as when introduced to captive conditions. Individual temperament may be an important factor in the success of conservation actions (McDougall et al., 2006). Therefore, we studied the personality types of European mink, with the aim of linking them to any behavioural problems observed during the mating season. As the first step, we addressed the question of whether it is possible to distinguish different personality types among a captive population of European mink. We performed a set of five experiments in two situations (non-breeding and breeding season, **V**).

2. MATERIAL AND METHODS

2.1. Study species: European mink

The European mink is a small semiaquatic carnivore that primarily inhabits small forest streams that do not completely freeze during winter. Their diet is comprised mostly of fish, amphibians, and crustaceans, but also includes small mammals (Maran et al., 1998; Sidorovich et al., 1998). The European mink was once spread throughout Europe, extending from the Ural Mountains to eastern Spain, and Finland to the Black Sea (Maran, 2007). Currently, the European mink is a critically endangered species (IUCN 2017) and one of the most endangered mammals in Europe (Temple and Terry, 2007). It is estimated that fewer than 5000 European mink persist in the wild, in less than 3% of their former range. The only remaining populations are in Danube Delta and in northern Spain (Maran et al., 2017), but even these populations are threatened by invasion of American mink (Macdonald and Harrington, 2003).

The decline of European mink has multiple causes in different regions and times, of which the introduction of American mink is just one. European mink started to vanish in central Europe as early as the end of 19th century. This was probably due to large-scale land-improvement and the dredging of rivers, which reduced the amount of suitable habitat. Declines in the first half of the 20th century in Eastern European countries (Poland, Hungary, the former Czechoslovakia), might be connected to the extensive development of agriculture, whereas in Finland it may have been caused by intensive hunting and active muskrat (*Ondatra zibethica*) trapping during the 1930s. In Estonia, major land improvements (e.g. the draining of small rivers) caused habitat loss, and thereby fragmentation of mink populations. European mink was still extant during the late 1980s in northern and eastern parts of Estonia, whereas in the south and west invasion of American mink had led to their local extinction. The last confirmed record of European mink is from 1996, after which wild populations have been regarded as extinct in Estonia (Maran, 1991). European mink had already experienced major declines before American mink were introduced in during the 1950s–1970s. This invasion of an alien mink was probably the terminal factor in the European mink becoming virtually extinct in Europe (Maran and Henttonen, 1995).

American mink were brought to Europe in the early 20th century as numbers of European mink were already too low for the fur-trapping industry and because of the comparatively higher value of American mink pelts. Introduction of American mink was not considered a threat to our native species as in those times they were not regarded as two distinct species (Maran et al., 2016b). American and European mink share the semi-aquatic habitat, and are similar in appearance and ecology despite the fact that they are not sister species. The American mink is even classified as belonging to a different genus, *Neovison* (Abramov, 2000; IUCN 2017). With respect to the diet of these two species, European mink are slightly more specialized than American mink, but their diet overlaps to a considerable extent (Sidorovich et al., 1998). When these two species coexist, then encounters are probably aggressive, dominated by the larger American mink, and could even result in the death of European mink (Põdra et al., 2013a). As a consequence, American mink force European mink to withdraw to suboptimal habitats, where the amount of prey might not be sufficient for females with a litter and reproduction may fail. This, in turn, induces further fragmentation and decreases population sizes (Sidorovich et al., 1999; Sidorovich and Macdonald, 2001).

In 1992, the European Endangered Species Program (EEP) for the European mink was launched by the European Association of Zoos and Aquaria (EAZA), to secure the survival of the species. The first goal was to establish a viable captive population that breeds regularly. The long-term aim of this programme was to maintain in European zoos and other breeding facilities 85% of the original heterozygosity of the founding individuals over 50 years. Fourteen different institutions participate in this programme, with an overall stock of 210 specimens (as of 31.12.2016). The coordinator of this program is Tallinn Zoo, wherein the largest captive population of European mink is located. The Tallinn population is based on 22 founders, which were obtained from Russia through collaboration with the Central Forest Biosphere Reserve (Tver, Vologda, Pskov, Novgorod and Leningrad Regions, Russia; Maran, 2003). The first breeding event occurred in Tallinn in 1986, but regular breeding was not achieved until the mid-1990s. Currently, the size of the population in Tallinn has stabilised at the near maximum level that the facility can sustain – 112 individuals, with genetic diversity (GD) retained at 93%, a generation time of 1.62 years, and an effective population size of 65.6 individuals (as of September 2017). Extension of the facility is limited mainly by a shortage of funds for new constructions, but also by the high costs (food, husbandry etc) of maintaining a high number of mink in captivity (Maran, 2003).

In addition to the preservation of the genetic diversity of the species in captivity, the EEP also serves as a source for mink reintroduction projects in Estonia. The aim is to ensure that at least some areas have extant European mink populations, and that they must stay inaccessible to American mink. This means reintroducing individuals into a sufficiently large area with suitable habitats to maintain a self-sustaining population of European mink. Preferably, this should be an island surrounded by distribution barriers that make the invasion of American mink impossible (Maran, 2003). In 1998, it was decided to establish a special island reserve for European mink on Estonia's second largest island: Hiiumaa. The island lies 22 km from the mainland and the habitats there should be able to accommodate about 100 individuals. After trapping out the American mink that had escaped from a fur farm that no longer exists on the island, the island was pronounced American mink free. The distance to the mainland is too far for American mink to spread there independently (Maran, 2003). In 2000, the first European mink were released onto the island and such introduction attempts have occurred annually ever since. So far (2000–2016), 578 animals have been released (Maran et al., 2016a). Monitoring radio-tracked European mink has revealed that released mink adapt to the wild and establish stable home ranges 1–1.5 months after release. Survival has been highest when the animals were maintained in large natural enclosures before release. The main causes of death have been predation by other carnivores (Maran et al., 2009). After years of purposeful work, there is now a small breeding population on the island (Maran et al., 2016a).

2.2. The captive population of European mink at Tallinn Zoological Gardens

2.2.1. Management of the captive population

All the studies included in this thesis were made at Tallinn Zoo. In Tallinn the captive European mink are housed individually in 2m × 2m × 4m enclosures, which are located side by side. The enclosures are separated by wire mesh walls with the lower parts covered by plywood to reduce visual contact between the animals. Each enclosure contains a nest box, a water pool (64cm × 35cm × 30cm) and several other items, such as branches, tree stumps, and tubes for the purpose of environmental enrichment. The animals are fed with rodents (frozen), fish, birds (chicks), or minced beef meat.

The animals are usually visited once a day, when they are fed and their enclosures cleaned. All animals are weighted once a month, when they are transported to and from a weighting room using a transport box. When the breeding season approaches, those females selected to be breed are regularly monitored for the onset of oestrus (**II**). When oestrus is detected, the male selected as a mate is introduced into her cage. The couples are observed for approximately an hour or until the copulation occurs, and then left together a few days (Papers **I**, **II** and **III**). Pregnant females and their future litters are left undisturbed in their enclosures until the cubs are about two months old, when they are separated from their mother (**IV**). At the beginning of September the litters are separated and all the cubs get their own enclosure.

While performing each of the studies, care was taken that the normal routine of the animals was not disturbed, or the changes were minimal. The well-being of the animals was always our first priority.

2.2.2. Data collection

The breeding data used in papers **I** and **III** were received from the European mink studbook database, maintained in the Single Population Analysis and Record Keeping System (SPARKS; www.species360.org). The purpose of this software is to assist in assembling, editing, analysing, and producing reports on the status of a captive population held at multiple facilities. The database contains individual data on each animal: time and place of birth, gender, parents, any movement between breeding facilities, breeding, offspring produced and time and place of death.

To analyse the reproductive success of females, data on all the litters females had produced over 20-year period was gathered from SPARKS. 165 different females had produced at least one litter during that time. To calculate juvenile mortality, data about deaths before an animal's first breeding season was also retrieved from that database. Information about the pedigree of each mink was also retrieved to calculate the heritability of litter size. The dataset covered 204 individuals (**I**). In paper **III**, the SPARKS database was used to find the number of successful and unsuccessful breeding events, to analyse the effect of mink origin on breeding success. The compiled data set contained information on 33 wild and 224 captive born mink.

In addition, data from the breeding database – updated annually by the research lab at Tallinn Zoo – were used in paper **I** to retrieve data about cubs born and cubs that survived until litter separation (at the beginning of September). In paper **III**, such breeding logs were used to gather information about all the mating attempts from 2004–2010 (N=579), to analyse the determinants of mating success. A breeding log is filled in per mating attempt, with the data recorded including the identity of the male and female, behavioural observations, and the outcome (successful or not).

Hormonal study

To determine seasonal hormonal profiles in pregnant and nonpregnant females (**II**), a non-invasive monitoring method was used. Faecal samples were collected over 16 months – to include two consecutive breeding seasons – from 15 females selected for breeding. Oestrogen and pregnane metabolite levels were measured using enzyme immunoassays following an established protocol for total oestrogen and 20-oxo-pregnanes. To study induced ovulation, three other females that were in oestrus were treated with human chorionic gonadotropin (hCG; Sigma C-1063; 90 IU, 0.36 mL, intramuscular) and faecal samples collected 15 days later. To correlate vaginal cytology for oestrus detection with faecal oestrogen metabolite measurements, faecal samples and vaginal smears were collected at one to three day intervals from March to May from 11 females that were not bred that year.

Litter behaviour

To study social behaviour during the juvenile period of European mink, 13 litters were observed 10 times over a two-month period. During each observation event, the litter was video recorded for 30 minutes from the top of the enclosure. The recordings were used to compile a detailed ethogram of social and solitary play behaviour of European mink cubs. Litters were disturbed as little as possible to avoid influencing their behaviour. Therefore, the pregnant females were placed into enclosures over which observation platforms had been built earlier. The litters stayed in the same enclosure over the whole period (**IV**).

Personality traits

To determine personality trait domains and examine how they are affected by situation and context, 80 animals were tested during autumn, and second time in spring before the breeding season (n=68). The animals were experimentally tested five times during both these periods: three times in their own enclosure, and twice in a novel environment. The animals were transported to a novel environment by catching them in a transport box, which is a standard procedure used also in connection to monthly for weighting.

Types of behaviour were scored only the first time they were observed, for example, when the animal first approached the novel object. We gave higher scores if the focal behaviour occurred early during the experiment. Individuals who, for example, attacked a novel object immediately, differed in their behaviour from individuals that dared to attack the object just before the end of the trial. The test period was 4 minutes divided into three 80 second periods. The number of points given depended on the period in which certain behaviour first occurred: 3 points in the first, 2 points in second, and 1 point in last period. Latency before the animal left the nest or transport box was measured in seconds (maximum 240 seconds; Paper **V**).

3. RESULTS

Reproduction

Breeding of European mink occurs during spring. Females come to oestrus from middle March to middle May, with the peak in April (**I**). When the first oestrus period remained undetected or the mating attempt failed, females could have another oestrus later in spring (**II**).

The gestation period was on average 43.8 days (±1.4 SD), the mode being 43 days. During the 20-year period, 267 litters were delivered, of 1171 total cubs. Average litter size was 4.42 (±1.48 SD), and the mode was four cubs. Eighty-five (7.3%) cubs died before their first mating season. Most of the deaths (n=79; 93% of all deaths) occurred before litter separation. The average number of juveniles per litter that survived to litter separation was 4.08 (± 1.48 SD), with 4.07 (± 1.5 SD) surviving to their first breeding season (**I**).

We analysed the determinants of reproductive success among females with the aim of providing recommendations for selecting which females to breed. We found that the age of the mother had a negative effect on litter size. However, the negative effect of age appeared only when the mother was older than four years: younger age classes did not differ in breeding success. The weight of the mother had a positive effect on the size of the litter. All the large litters (> 6 cubs) were produced by females that were heavier than 650g. We also found that the weight of mothers increased over the 20 years of the programme. We did not find any signs of the cost of reproduction: the number of litters a female had delivered earlier in her life did not have an effect on her litter size in the focal year; the number of cubs born and number of cubs survived were not affected by the mothers reproductive history from the preceding year. When the effects of age and weight were accounted for, individual females did not vary in terms of litter size, also the heritability of litter size was estimated to be low (**I**).

Hormonal study

With the aim of improving the breeding success of European mink, a detailed study of oestrus, ovulation and pregnancy was conducted. The overall pattern of total oestrogen and 20-oxo-pregnane in pregnant and nonpregnant animals followed a seasonal profile. During the breeding season, the mean oestrogen metabolite level was elevated as compared to before the onset of the breeding season. After conception, both oestrogen and 20-oxo-pregnane concentrations increased. Both metabolites reached the highest levels during gestation. After treatment with hCG, 20-oxo-pregnane levels increased resembling the hormonal profile of pregnant females. During lactation, 20-oxo-pregnane metabolite levels were higher than in nonpregnant females. Litter size was correlated with 20-oxo-pregnane levels but not with oestrogen (**II**).

Mating success

By comparing the breeding success of wild and captive born males, we found wild born males were significantly more successful than captive born males (success rate 89% and 35%, respectively). Hence, the poor breeding success should primarily be attributed to males born in captivity (**III**). In the detailed study of the data on mating attempts, we determined that male aggressive and passive behaviour were both primary causes of mating failures. We revealed that mating success, males' aggressiveness and passivity depend more on the male than the female partner. Additionally, we did not find any evidence that the behaviour of an individual was dependent on the identity of its partner. We concluded that passivity and aggressiveness are both alternative expressions of males' behavioural inability to mate. Aggressively behaving males are passive in non-aggressive situations and *vice versa* (**III**).

Behaviour of cubs during the litter period

To study the social behaviour of the cubs, 13 litters were observed during active times that amounted to a total of 3900 minutes of surveillance (**IV**). Overall, the most frequent type of behaviour was social play. Among the different litters, an approximately equal share of time was spent on social play. The play itself was diverse, containing all the different elements described in related species. We did not reveal any significant association between the time spent on biting and the age of the litter. Only the social play of the cubs (excluding bites) decreased significantly over time and the pattern was similar across the litters. There was a significant change in the duration of mothers' behaviours with litter maturation: the duration of mothers' play with the litter decreased and aggressive behaviour of the mother increased. We also found a positive correlation between time cubs spent biting siblings and mothers' play with the litter (**IV**).

Personality traits

During the study in which we assessed personality types, the behavioural measurements obtained from the tests were grouped into three factors, which taken together explained 55.9% of the variance (**V**). The first domain was called "boldness" as it was related to behaviours such as "approach to object" and "latency to leave the nestbox in the presence of a novel object". The second domain was mostly related to responses to the mirror image of the animals in the novel arena, such as "looking at and sniffing the mirror image", or "marking the area". It seemed to be related to non-aggressive social behaviour outside the animal's own territory. Therefore, this domain was called "sociability". The third domain was associated with explorative behaviour in the novel environment such as "number of zones visited in a novel arena", "hissing", "marking" and "digging". This factor was called "exploration".

The scores of all these three personality trait domains were repeatable between the seasons. Between the seasons, gender had a significant relationship with boldness and there was a significant interaction between gender and season in terms of boldness. Whilst males got bolder females got shyer with the breeding season approaching (**V**).

4. DISCUSSION

Overall, management of the captive population of the critically endangered European mink at Tallinn Zoo has been successful. A considerable amount of offspring (1171 cubs) have been born during the 20-year period (1996–2015). Mortality of the cubs has been minimal (85 cubs), with most cubs surviving until their first breeding season. An overview of the date of the onset of the breeding season, gestation period, average litter size, and litter mortality was given in our study (**I**) that involved a much larger sample size compared with earlier studies (Amstislavsky et al., 2009; Ternovskii, 1977) but the results were similar. Gestation period did not differ much from that of related species: it was similar to the European polecat (*Mustela putorius*), the steppe polecat (*M. eversmanni*; Nowak, 2004), and the black-footed ferret (Williams et al., 1992).

The average size of captive European mink litter was 4.4 (**I**) which is close to the value reported from Russia (4.7) by Danilov and Tumanov (1976), although these values are higher than those of wild population in Belarus (3.8; McDonald and Harris, 2002), and France and Spain (3.4; Fournier-Chambrillon et al., 2010). Consistently, when comparing the data about the litter sizes of related black-footed ferret then in captivity it was larger (3.4 cubs; Vargas and Anderson, 1998) than in nature (3.17 cubs; Ayers et al., 2014).

In female European mink, the hormonal profiles during the different reproductive stages were described and the hormonal differences between pregnant and nonpregnant females analysed (**II**). The results were in accordance with the earlier conclusion that European mink is a seasonally polyestrous species (Amstislavsky et al., 2009). The European mink is regarded as an induced ovulator, as are many other mustelids such as the polecat, black-footed ferret, river otters and the sable (Chang and Yanagimachi, 1963; Mead et al., 1988; Rozhnov et al., 2008; Stenson, 1988). The results of this study support this assumption because 20-oxo-pregnane levels did not increase in females that were not mated. Furthermore, 20-oxo-pregnane levels increased in hCG-treated females, closely resembling hormone profiles of pregnant females during the first 2 weeks of gestation. This indicates that hCG can be applied to induce ovulation and perhaps using as a new tool to support population management of the European mink. This has been successfully used in black-footed ferret (Howard et al., 1997) and domestic ferret (Chang, 1968).

An essential criterion of the successful management of a captive population is a sufficient number of offspring produced annually. Thus, per female mammals, the litter size and offspring survival are the parameters of primary interest, and predicting these is thus of a high practical value. We revealed that the most important factor influencing female minks' reproductive output was age, but only when the female was older than four years (**I**). The fact that the litter size decreases in time when the animal gets older is shown also in similar species like captive and wild American mink (Koivula et al., 2010; Melero et al., 2015). Nevertheless, in our study the litter size was not age-dependent in younger than five year old females, which is in contrast to the findings in American mink (Koivula et al., 2010).

We also found a positive association between litter size and the weight of females (**I**), which has also been shown among various other species. The relationship between body weight and reproduction is mainly explained by variation in the nutritional status of the breeding animals (Frynta et al., 2011; Gese et al., 2016; Persson, 2005). We noticed that the body weight of European mink increased by approximately 10% over 20–years of observation. We hypothesise that this was likely the result of an improvement in the quality of the food provided to the animals, but unfortunately, the older nutritional data are too incomplete to test this. Nonetheless, the phenomenon of changing body weight among long-term captive population certainly requires future study.

In our study population, we found no evidence of the cost of reproduction (**I**). In the literature, it has been suggested that the cost of reproduction should be more apparent when the life-history trait in focus has a high variance. This is typically the case in long–lived species, to which the European mink can be considered to belong. Therefore, we probably could find some evidence of the cost of reproduction in wild European mink populations. In other members of the Mustelidae, the existence of reproductive costs have been reported, e.g. among wild American mink (García-Díaz and Lizana, 2013) and wild wolverines (Persson, 2005). We suggest that the high quality and constant availability of food in captivity eliminates the physiological mechanisms behind the cost of reproduction, so that a failure to observe this phenomenon should not be surprising. As a summary of these results, we suggest that when selecting females for breeding, there is little need to consider aspects other than genetic relatedness (**I**).

Captive populations of endangered species are mostly rather small in number and have minimal or non-existent immigration. Due to genetic drift, such populations are expected to randomly lose alleles. This can lead to significantly reduced genetic diversity and leave most of the loci in the homozygotic state, resulting in inbreeding depression (Frankham, 2010). Therefore, it is essential that all designated animals, which have been selected for breeding, with the aim to maintain maximum genetic diversity, will actually reproduce. Unfortunately, problems with breeding are common among captive species (Abello et al., 2011; Carlstead et al., 1999; Martin and Shepherdson, 2012). In paper **III**, the records of mating behaviour were examined. It was revealed that breeding failures mostly occur due to the abnormal behaviour of captive born males: some behave passively or are aggressive. In less than one third of the mating attempt studied, the males behaved normally, i.e. mated with the female. In most those cases, the female delivered a litter (**III**).

Problems with mating behaviour in captivity are common among many carnivorous (Wielebnowski et al., 2002; Wolf et al., 2000; Zhang et al., 2004). The suggested reasons of limited success include physiological problems (Wolf et al., 2000; Zhang et al., 2004), improper keeping conditions and environments with too low complexity (Diez-Leon et al., 2013; Zhang et al., 2004). In addition familiarity with the breeding partner can play a significant role (Peng et al., 2009). The distortion of reproductive behaviour is frequently expressed as abnormal mating behaviour and it is often difficult to determine the causes (Coelho et al., 2012; Wolf et al., 2000). We can only suppose that the causes are associated with the captive environment and the conditions which exist there.

The early environment of an animals' life can cause a long–lasting effect on the individual's ontogeny (Hudson et al., 2011). As the behaviour of the European mink litters have not been described earlier, we compiled a detail ethogram of social behaviour among European mink litters. Their social behaviour was found to be complex (**IV**) and the behavioural acts observed closely resembled those reported for related species (Clark et al., 1986; Poole, 1966, 1967, 1978). This could indicate that the environmental conditions in enclosures are sufficiently variable and "normal" that young animals will and can perform different kind of play elements (Nogueira et al., 2011; Talbot et al., 2014).

We found that the most frequent type of behaviour during the litter period of the European mink was social play. Time spent on biting (which could indicate to aggressive behaviour) did not increase over time. The behaviour of the mother did change over time: the share of caring and playful behaviour decreased when the cubs grew older, and she also became more aggressive. Her aggressive behaviour became so frequent that we had to separate the mother from the litter to prevent injuries she could cause to her cubs. Likely, such an increase in the aggressive behaviour of the mother was associated with the litter dispersal. When the cubs got old enough they should start to seek their own territories and the mother's aggressive repulsing behaviour might encourage them to do so. Therefore we think that the change in the behaviour of the mothers was normal and would probably also happen in nature. In general, we found that the behavioural repertoire of captive-bred European mink litters was complex and consisted of all expected elements. We did not find litters with significantly differing behaviours and no unexpectedly high aggression was found. Therefore, we can conclude that our study did not reveal any juvenile behavioural distortion in European mink captive population (**IV**).

An increasing number of studies report the existence of personality types among various nonhuman species (Cheng et al., 2017; Kanda et al., 2017; Lehmkuhl Noer et al., 2016). In the case of the European mink, there might well be some environmental or management factor that affects some animals, so that their will develop abnormal mating behaviour. We identified personality types among European mink for the first time. These types were designated as boldness, sociability and exploration. We found them to be individual-specific and repeatable both within and across seasons. These results gave us an important knowledge base to test for possible relationships between these types and male reproductive behaviour in captivity (**V**).

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Summarizing the results from the perspective of *ex-situ* species conservation, I would highlight the following:

- at Tallinn zoo, fecundity and juvenile survival of European mink has been high compared to other available data on this and related species. General conditions at the zoo can therefore be considered appropriate, with little need for further improvements;
- there is little variance in the reproductive success of individual females. Females used for breeding can therefore be selected solely using the criterion of maintaining maximal genetic diversity;
- the main bottleneck threatening the success of the *ex-situ* breeding programme is the abnormal mating behaviour of captive born males;
- even if the reason for behavioural problems has often been in the social environment experienced during the juvenile development, the present study did not find any evidence of that in the case of the European mink.

Based on our results, I wish to outline several issues which deserve to be studied further.

- Even if there was nothing „suspicious" in the behaviour of juvenile European mink (**IV**), it would greatly help to obtain data on the behaviour of the juveniles and their parents in nature as a comparison.
- Also, I suggest focusing on the phenomena related to litter dispersal. This stage of their life cycle has unfortunately not been studied in detail, and no species-specific information exists regarding wild populations. However, some attempts along this stage have been made with captive European mink in Germany (Festl et al., 2003). The results indicate that social contacts with littermates persist after litter separation which may play an important role in the development of normal social behaviour in adulthood. Therefore, different timing and methods of litter separation should be studied in relation to future mating success.
- In our third paper (**III**), we found that being captive born is the main correlate of not mating normally. It has been demonstrated that environmental enrichment reduces stressful behaviours among captive American mink and improves their mating performance (Diez-Leon et al., 2013). It has also been found that the environmental enrichment is most important for young male black-footed ferrets as their stress level was reduced at most compared with other age classes and sexes (Poessel et al., 2011). We suggest that young European mink males should be hosted straight after litter separation in large, environmentally rich enclosures, and the effect of such treatment on mating success analysed.
- Even though we did not find evidence that mating success depends on the female partner, the effect of mate preference should be studied. It has been shown that mate preference positively affects copulation success, litter size

and offspring survival (Martin and Shepherdson, 2012; Martin-Wintle et al. 2015). We should compare reproductive success between females mated with a male from a neighbouring enclosure to success with males from a non-neighbouring enclosure, and between females mated with preferred and non-preferred neighbours. Preference should be determined based on behavioural interactions between the animals.

- The results of the fifth paper (**V**) suggest the need for even more thorough studies of individual behaviour. The methods used to determine the personality types of mink can be applied in future studies, consistent with the suggestions that captive breeding programmes should, beside genetics, also consider individual temperament when deciding on the selection of breeding pairs. Actions that ignore personality can lead to the captive population developing towards domestication through unintentionally favouring some types of temperament. This may affect the success of captive breeding programmes and future reintroduced populations (McDougall et al., 2006). Using results of paper **V,** we could develop an express method to quickly determine personality types, with the potential of using this information as part of a management protocol.
- The revealed increase in the weight of *ex-situ* females and the correlated increase in litter size (**I**), should be examined in the context of the effect of these temporal trends on mating success, health, and future reintroduction strategies.

SUMMARY

Saving critically endangered species from extinction is the main goal of *ex-situ* conservation methods. Such methods are frequently inevitable, even when removing animals from their natural habitat and bringing them into an artificial environment is a difficult way to achieve this goal. Experience obtained from successfully managed populations is extremely important to ensure the success of other such programmes. The important and delicate events of animals' lives such as mating, gestation, birth and the litter period are also the most problematic in captivity.

In this thesis I gave an overview of European mink behaviour and reproduction. The results suggest practical actions to improve the breeding success of this species, and form the basis for future studies on captive European mink population.

At present, the most critical aspect of the captive breeding programme of this species is ensuring high mating success. We revealed that the main reason why breeding fails is due to the number of captive born males with inadequate (i.e. aggressive or passive) behaviour during the mating attempt. We found that mating success depends more on the male than on female partner (**III**). The females' hormonal profiles were analysed and no abnormalities were found (**II**). Females' breeding success in terms of litter size depends mainly on the age and weight of the animal, which corresponds to a pattern which is perhaps universal among mammals. No signs of reproductive cost were found. This was probably due to the high quality and always available food in captivity which might eliminate the physiological mechanisms behind the cost of reproduction (**I**).

Abnormal behaviour could develop due to an unsuitable environment during early life stages. As the social behaviour of the European mink litters were completely undescribed, a detailed ethogram of play behaviour during the litter period was compiled. The observed play was diverse and contained all behavioural acts described in related species. None of the litters were characterised by deviating behaviour and we found no evidence of unexpected aggressive behaviour. Therefore, our results do not provide evidence of behavioural distortion among captive European mink cubs (**IV**).

As advised in the literature, keeping a population in captivity should rely more on individual-based approaches. We determined three personality trait domains among the European mink captive population: boldness, sociability and exploration. We demonstrated that the situation and context influences the expression of personality trait domains and plasticity can be large, but that the concept of personality type remains applicable due to the repeatability of the measurements. Establishing different personality traits among mink shows that animals do differ in their behaviour in a consistent manner. These behavioural differences may affect the way individuals interact with the environment which may also lead to an inability to display proper behaviour during mating attempts (**V**).

As management of species in captivity is a challenging task, any salient knowledge published about other species is of high value, and can become most useful throughout the wide area of *ex-situ* conservation.

KOKKUVÕTE

Ohustatud Euroopa naaritsa (*Mustela lutreola*) sigimine ja käitumine tehiskeskkonnas

Ohustatud loomaliigi kaitsmine väljaspool tema looduslikku elupaika (*ex-situ* liigikaitse) võetakse ette enamasti alles siis, kui ülejäänud võimalused tema väljasuremise vältimiseks on ammendatud. Kahjuks on taolise meetodi edukus väga madal, lisaks on ta keeruline ja kallis. Seda eelkõige seetõttu, et loomad on vaja välja püüda nende looduslikust keskkonnast ning tagada neile edukas toimetulek uudsetes tingimustes. Hoolimata raskustest on *ex-situ* liigikaitse pahatihti ainuke ja viimane sobiv lahendus. On mitmeid näiteid, kus taolise tegevusega on edu saavutatud: kadumas olnud liigi populatsioon on taas loodusesse asustatud. Selliste edukate ettevõtmiste käigus omandatud kogemus ja teadmised on äärmiselt olulised analoogiliste projektide õnnestumise tagamiseks.

Käesolevas doktoritöös keskendume ühele kriitiliselt ohustatud imetajaliigile, Euroopa naaritsale. Naarits oli varasemalt levinud peaaegu üle kogu Euroopa, kuid nüüdseks on säilinud vaid mõned üksikud, kahaneva arvukusega populatsioonid. Liigi kadumise peamisteks põhjusteks olid üleküttimine, sobivate elupaikade vähenemine ja Ameerika naaritsa invasioon. Kindlustamaks liigi edasikestmist loodi tehiskeskkonda naaritsa populatsioon. Eesmärgiks on loomi paljundada, alal hoida veel alles olevat geneetilist mitmekesisust ja taasasustada naaritsaid neile sobivatesse elupaikadesse looduses.

Tehistingimustes peetava populatsiooni käekäigu seisukohalt on eelõige olulised sigimishooaeg, tiinus, poegimine ja pesakonnaperiood. Paraku on eelnimetatutega seotud ka kõige suuremad probleemid. Nii on see ka Euroopa naaritsa puhul: kõige problemaatilisem on edukas sigimine. Paljud loomad ei saa järglasi, mistõttu populatsiooni geneetiline mitmekesisus langeb murettekitava kiirusega.

Euroopa naaritsa paljundusprogrammis on praegusel hetkel kõige kriitilisemaks piisava paaritumisedukuse tagamine. Käesolevas töös leidsime, et eelkõige on võimalik sigimisprobleeme seletada isaste naaritsate ebaadekvaatse käitumisega paaritumiskatses. Nimelt käitub osa vangistuses sündinud isastest sigimishooajal ebanormaalselt, s.t. on emase vastu agressiivne või jääb passiivseks ega ilmuta huvi partneri vastu (**III**). Uurides emaslooma suguhormoone, leidsime, et kõik on normaalne ja hormonaaltsükkel järgib naaritsal ja teistel lähedastel liikidel eelnevalt kirjeldatud rada (**II**). Emaste sigimisedukus, mida kirjeldasime läbi pesakonna suuruse ja poegade ellujäämuse, sõltus eelkõige emase vanusest ja kaalust. Sellised seosed on imetajate hulgas üsnagi universaalsed. Lisaks otsisime tõendeid sigimise hinnast naaritsa tehiskeskkonnas peetaval populatsioonil, kuid neid me ei leidnud. Kuna mitmetel sarnastel looduses elavatel liikidel on sigimise hind tõendatud, siis eeldasime, et kõrge kvaliteediga toidu pidev kättesaadavus mõjutab neid füsioloogilisi mehhanisme, mis mõnes teises olukorras sigimise hinda põhjustaksid (**I**).

Ebanormaalne käitumine võib areneda varajases eluetapis kogetud ebasobiva keskkonna tõttu. Euroopa naaritsa poegade sotsiaalset käitumist ei ole varem kirjeldatud. Koostasime mängukäitumise detailse etogrammi, st nimekirja käitumisaktidest, mida noorloomade mäng sisaldab. Naaritsapoegade käitumine oli mitmekesine ja sisaldas kõiki käitumisakte, mis on kirjeldatud ka sugulasliikidel. Ühtegi pesakonda ei saanud iseloomustada kui käitumiselt hälbivat ning me ei leidnud ka tõendeid ebanormaalselt agressiivsest käitumisest. Seetõttu ei paku meie tulemused tõendeid käitumuslikust ebanormaalsusest vangistuses peetavatel Euroopa naaritsa poegadel (**IV**).

Üha rohkem hakatakse pöörama tähelepanu sellele, et tehiskeskkonnas peetavate populatsioonide majandamine peaks sisaldama rohkem isendipõhist lähenemist. Tegemaks algust taolise tegevusega, määrasime loomaaia naaritsate iseloomutüübid. Eristasime kolm iseloomu mõõdet: julgus, sotsiaalsus ja uurivus. Näitasime, et situatsioon ja kontekst mõjutavad iseloomutüübi ilmnemist ja plastilisus on seega suur. Siiski saab tänu mõõtmiste kõrgele korratavusele rääkida naaritsate iseloomutüüpidest (**V**).

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Kiik, K., Maran, T Nagl, A., Kneidinger, N., Tammaru, T. "Behavioural studies of critically endangered European mink (*Mustela lutreola*) in captivity", Behaviour 2017 – 35th International Ethological Conference, Estoril, Portugal 30.7–04.08.2017, oral presentation

Kiik, K., Tammaru, T., Kneidinger, N., Maran, T. "Behavioural interactions in European mink, *Mustela lutreola*, captive-bred litter – implications to conservation", The Nordic Evolutionary Psychology Meeting 2013, 12–13.09.2013, Tartu, Estonia, poster presentation

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Kiik, K., Maran, T., Nagl, A., Ashford, K., Tammaru, T. "Breeding success of European Mink (*Mustela lutreola*) in captivity", The 3rd European Congress of Conservation Biology, 'Conservation on the Edge', 28.08.2012–01.09.2012, Glasgow, Scotland, UK, poster presentation

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Konverentsi ettekanded:

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