RESEARCH ARTICLE

The Causes of the Low Breeding Success of European Mink (*Mustela lutreola*) in Captivity

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High among-individual variation in mating success often causes problems in conservation breeding programs. This is also the case for critically endangered European mink and may jeopardize the long-term maintenance of the species' genetic diversity under the European mink EEP Program. In this study, breeding success of wild and captive born European minks at Tallinn Zoological Garden are compared, and the mating behavior of the males is analyzed. Results show that wild born males successfully mate significantly more often than captive born males (89% and 35%, respectively). On the basis of an extensive record of mating attempts, both male aggressiveness and passivity are identified as primary causes of the observed mating failures. All other potential determinants have only a minor role. Mating success as well as a male's aggressiveness and passivity are shown to depend more strongly on the male than the female partner. We did not find any evidence that the behavior of an individual is dependent on the identity of its partner. We suggest that aggressiveness and passivity are two expressions of abnormal behavior brought about by growing up in captivity: the same individuals are likely to display both aggressive and passive behavior. The results point to the need to study and modify maintenance conditions and management procedures of mink to reduce the negative impact of the captive environment on the long-term goals of the program. Zoo Biol. XX:XX–XX, 2013. © 2013 Wiley Periodicals Inc.

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INTRODUCTION

A biodiversity crisis is underway. According to recent reports, approximately 21% of extant mammal species are classified as threatened [IUCN, 2012; www.iucnredlist.org]. Despite this gloomy picture, recent analyses show that conservation efforts can and do make a difference. According to Hoffmann's [2010] calculation, in situ conservation efforts have played a role in the case of 7% of species (68 of 928; for birds 1988–2008, mammals 1996–2008, and amphibians 1980–2004) whose threat level has been recently reduced [Hoffmann et al., 2010]. Sometimes efforts in situ alone are not sufficient to secure the survival of an endangered species [Witzenberger and Hochkirch, 2011]. Here, ex situ conservation breeding can play an important role and has proven to be effective [Seddon, 2010; Conde et al., 2011]. A number of cases exemplify the role conservation breeding can have in securing the survival of species [Pereladova et al., 1999; Alcaide et al., 2010; Biggins et al., 2011; Lindsey et al., 2011; Zafar-Ul et al., 2011]. Managed captive populations act also as survival insurance for endangered species. Even after ultimate extinction in the wild, properly managed ex situ populations provide an opportunity to restore wild populations to existing empty habitats [Conde et al., 2011].

A prerequisite of success in conservation breeding is that all the animals of reproductive age can be used for breeding when needed [Price, 1999]. However, this is not always the case. Captive breeding programs are often plagued by a mortality rate that is too high or irregular breeding [Wolf et al., 2000; Dalerum et al., 2006; Hawkins and Battaglia, 2009; Peng et al., 2009], supposedly resulting from

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insufficient knowledge of species-specific behavioral and physiological requirements, or insufficient attention to such requirements [Zeoli et al., 2008]. Several studies have reported that abnormal mating behavior such as aggressive/passive behavior toward potential mating partner is to be blamed for poor breeding success [Wolf et al., 2000; Zhang et al., 2004; MacKinnon et al., 2008]. Such abnormal behavior has been reported to be caused by too small and/or too homogeneous furnishing of the enclosure, presence of natural enemies or humans, or social stress caused by the physical presence of too many conspecifics [Price, 1999; Peng et al., 2007].

The European mink (*Mustela lutreola*) is a critically endangered species according to the IUCN Redlist 2012 [IUCN, 2012; www.iucnredlist.org] assessment and one of the most endangered mammals in Europe [Temple and Terry, 2007]. Indeed, the species has disappeared from most parts of its former range. The main factors contributing to this extinction are habitat loss, over-hunting, and the invasion of a dominant competitor, the American mink [Maran and Henttonen, 1995; Maran, 2003, 2007; Maran et al., 2004].

In 1992, the European Endangered Species Program (EEP) for the European mink was launched by the European Association of Zoos and Aquaria (EAZA). The aim of this program is to maintain—in European zoos and other breeding facilities—85% of the original heterozygosity of the founding individuals for 50 years. Currently, there are 218 mink in captivity under the EEP program. Nearly half of the captive population of European Mink is held at Tallinn Zoo, Estonia, the population is based on 22 founders. Currently (as of December 31, 2011) the size of the population is $n = 110$ individuals, genetic diversity (GD) retained is 93%, generation time 1.62 years and effective population size 65.6 individuals. In addition to the preservation of the genetic diversity of the species in captivity, the EEP Program also serves as a source for a mink reintroduction projects in Estonia (on the islands of Hiiumaa and Saaremaa) as well as in Germany [Maran et al., 2009].

In the framework of the European mink EEP program, all known breeding events in the captive population have been recorded. Furthermore, since 2004, the behavior of mink during mating attempts has been recorded at Tallinn Zoological Garden. These two sets of data provide us a unique opportunity to look into the effect of mating behavior on the breeding success in captivity. In this manner, we are forming an initial insight into the role of abnormal mating behavior in breeding failures of the European mink. In particular, our study aims to answer the following question: Which traits of the male and the female (such as origin, sex and partner identity, as well as age, number of mating attempts in 1 year) are the main determinants of mating success?

MATERIALS/METHODS

Captive Population and Its Management

At Tallinn Zoo, all animals are housed individually in 20-animal "modules," aligned in two rows with 10 enclosures ($2\,m \times 2\,m \times 4\,m$) in each. The rows are separated by a service corridor. The enclosures are separated from each other by double welded, wire mesh walls. Lower parts of the wall are covered by plywood to reduce visual contact between the animals. The enclosures are cleaned and the animals are fed daily.

The Effect of Origin on Breeding Success

The effect of mink origin (wild or captive) on breeding success was analyzed on the basis of the pedigree data being accumulated in the SPARKS database (www.isis.org). From the 1980s until 2003, the main goal of the program had been to increase the size of the captive population and therefore every animal was involved in the breeding program. Therefore we assumed that any animal which left no offspring was an unsuccessful breeder. Breeding records and the data about the origin of bred mink until 2003 (both wild and captive born) were used in the analyses.

Mating Trials

A detailed analysis of the determinants of mating success could be conducted on the basis of breeding logs which had been kept at the Tallinn Zoological Garden since 2004. By that time, all animals were captive born. From 2004 to 2010, all mating attempts were kept track of and classified as successful or not. Mating attempt was classified successful if copulation was observed. Also, cases of aggressive or passive behavior were recorded. Aggressive behavior was defined following to Poole [1966], that is, a study on the related European polecat. A male was considered passive if he did not show any interest towards the female (started to forage, explored the area, receded into nestbox and stayed there). Additionally, the logs contained basic information (such as age) concerning every individual involved.

A mating trial was initiated when a female reached oestrus, and a designated male partner was placed in her cage. The selection of male partners was based on the analyses conducted with the PM2000 software [Pollak et al., 2002]. An observer monitored the couple until copulation occurred. Subsequently, the animals were left to stay together for a few days. The trials with no copulation lasted one hour after which the animals were separated. In the cases of aggression, the trials were terminated and the animals were immediately separated to avoid injuries to the female. In such trials, the male was scored as having behaved aggressively in the particular mating attempt. If the attack was not very serious and thus the female was not particularly disturbed, the trial was continued for the predetermined time (1 hr), but the male was still scored as having behaved aggressively. The animals were also separated after an hour of observation if the male was acting passively, that is, if the male did not pay any attention to the female. In these cases, the male was scored as passive for that breeding attempt.

To find out the effect of aggressive or passive behavior of the male on mating success, the latter (as a binary variable:

TABLE 1. Independent variables used in the analyses to explain the variation in mating success

Effect	Level of variation	Mean	SD	Min	Max
Male					
Aggression index[a]	i	0.26	0.35	0	1
Passivity index [a]	i	0.35	0.38	0	1
Age[b]	ma	2.02	1.3	1	9
Attempt[c]	ma	2.72	2.04	1	13
Female					
Experienced passivity[d]	i	0.27	0.27	0	1
Experienced aggressiveness[d]	i	0.13	0.19	0	1
Age[b]	ma	2.9	1.8	1	9
Attempt[c]	ma	2.68	1.86	1	9
Earlier experienced aggressiveness[e]	ma	0.4		0	1
Earlier experienced passivity[e]	ma	0.6		0	1

Some variables varied at the level of particular mating attempts (ma) while some had values attached to particular individuals (i).[a]Aggression index (mean aggressiveness) of each particular male was presented as the share of the male's aggressive attempts from the number of all his mating attempts in the data base (0, never aggressive; 1, always aggressive). Passivity index (mean male passiveness) was calculated analogously.[b]The age of the animal at the moment of the mating attempt (years).[c]Order number of the mating attempt. For each male the numeration starts from one every breeding season and increases by one with every mating attempt. An analogous index for the female was calculated similarly.[d]Mean female experienced aggressiveness was presented as the share of mating attempts in the data set in which the male partner had been aggressive. Mean experienced passivity was calculated analogously.[e]Earlier experienced aggressiveness is a binary variable telling if the female partner has, or has not, previous experience with an aggressive mating attempt. Earlier experienced passivity has an analogous meaning.

copulation observed or not) was analyzed as dependent on "aggression index" or "passivity index" of the male (see Table 1 for definitions of variables). In the analyses, each mating attempt was treated as one observation. Several additional independent variables were included in the model (Table 1). For example, it is reasonable to assume that the previous mating experience of the female (having encountered an aggressive/passive male earlier or not) can affect the outcome of an on-going mating attempt, assuming that a female's behavior has some impact on mating success at all.

In order to check whether aggressive males tend to act normally or rather passively in those mating attempts in which aggressive behavior does not occur, the analysis was repeated on a reduced data matrix. In particular, the trials in which the male was acting aggressively were excluded. The relationship between mating success or passive behavior (both binary variables) and the male's "aggression index" was analyzed in a model with the same set of additional independent variables (Table 1). An analogous analysis was conducted to study the behavior of passive males during their non-passive breeding attempts. That is, the relationship between mating success or aggressive behavior and the male's "passivity index" was studied using the data matrix with all the passive attempts omitted.

In all analyses with a binary dependent variable (successful/unsuccessful; aggressive/nonaggressive, etc.) mixed generalized linear models were applied. Statistical analyses were performed with SAS/STAT 9.2 (SAS Institute, Inc., Cary, NC) software using the procedure *glimmix*. Male and female identities were used as random factors. Degrees of freedom were estimated using the Kenward–Roger method [Littell et al., 2002] to avoid overestimation—due to repeated measurements on particular individuals.

RESULTS

The Effect of Origin on Breeding Success

There was a significant ($\chi^2 = 38.3$; df = 1; $P < 0.001$) association between the origin (wild vs. captive born) of male European minks: 23 out of 201 captive born males had successfully bred at least once in their lifetime (11%), while wild born males respective numbers were 13 out of 20 (65%; Fig. 1). For females, no such association was found ($\chi 2 = 0.02$; df = 1; $P = 0.89$): 100 out of 229 captive born females (44%) bred at least once successfully. The corresponding figures for wild born females were 7 and 15 (53%), respectively (Fig. 2).

Aggressive and Passive Behavior in Mating Attempt

Our final matrix for 2004–2010 contained data on 579 mating events, 147 (25%) of which were classified as successful. There were data on mating attempts of 96 males

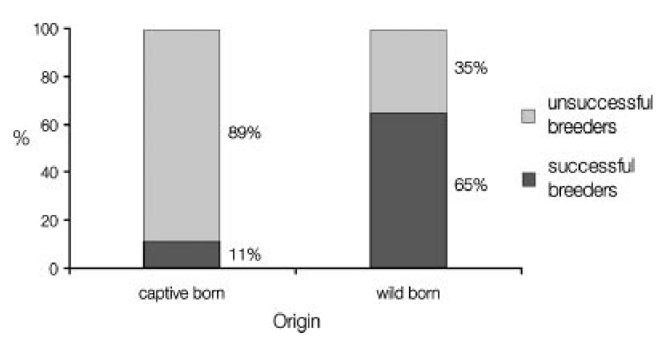

Fig. 1. Wild and captive born male European minks with successful breedings at least once in their lifetime.

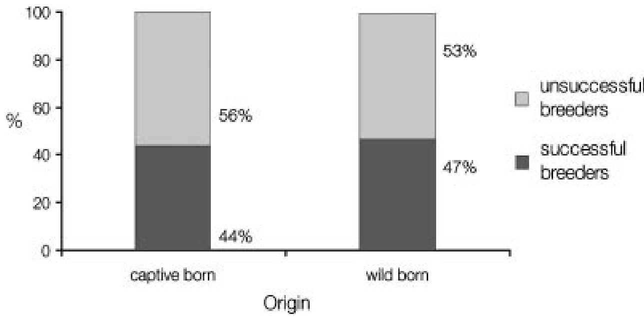

Fig. 2. Wild and captive born female European minks with successful breedings at least once in their lifetime.

and 84 females. Males were recorded to be aggressive on 103 occasions and passive during 203 mating events. Of all failed mating attempts (432), 24% were judged to have been unsuccessful because of aggressive behavior of the male partner, whereas in 47% the cause was passive behavior of the male, that is, a failure to be interested in the female. Only four aggressive trials resulted in successful mating. In total 67% of studied males failed in every mating attempt in their life (64 of 96).

As judged on the basis of estimates of among individual variance, and respective standard errors, mating success, as well as the occurrence of both aggressive and passive behavior, depended remarkably more on the male than the female participant of the mating event (Table 2). No evidence was found that the behavior of an individual was dependent upon the identity of its partner: the female by male interaction term was estimated to be zero for mating success, aggressiveness and passiveness in analyses analogous to those in Table 2.

To study the determinants of mating success (as a binary variable, one value for each mating attempt), generalized linear models with 10 independent factors (Table 1) were fitted first. The model was subsequently simplified in a stepwise manner so that only statistically significant effects remained (Table 3). Indeed, both the passiveness and aggressiveness indices of the male were the primary determinants of mating success, whereas similar indices calculated for the female partner had a weaker though still a statistically significant effect.

TABLE 2. Estimates of the effects of individual males (±SE) and females on the outcome of each mating attempt (a binary variable: successful or not) as provided by generalized linear model with male and female identity as random factors

Dependent variable	Estimate of variance	SE
Mating success	Female 0.202	0.207
	Male 2.01	0.51
Aggressiveness	Female 0	Not estimable
	Male 0.75	0.34
Passivity	Female 0.056	0.11
	Male 1.61	0.41

There were no fixed factors in the model.

However, our analyses described above contained a certain element of potential logical circularity. Indeed, as most mating failed because of a male having been either aggressive or passive, one may argue that a relationship between mating success and abnormal male behavior might partly result from the actual definition of successful mating. To overcome this problem, we re-scored male aggressiveness and passiveness as binary variables (e.g., the value one of aggressiveness was assigned to a male if he had been observed to behave aggressively at least once). Thereafter, we omitted these particular mating events which had served as the basis of such judgment (i.e., mating events in which a male had first been observed to be aggressive or passive) from the database, and repeated the analysis (Table 3). The results were not qualitatively different. Male aggressiveness and passiveness retained its statistically significant effect on mating success (Table 4).

Additionally, we tested whether a male which tends to be aggressive is likely to behave passively on those occasions it happens not to be aggressive, and vice versa. For this purpose we created a subset of data with all aggressive matings excluded, and found that both mating success ($F_{1,137.3} = 12.97$; $P = 0.0004$, in an analysis analogous that in Table 3) and passiveness ($F_{1,156.4} = 9.03$; $P = 0.0031$) were, indeed, higher in the more aggressive males. Analogously, in a data subset with passive mating occasions excluded, the passiveness score of a male negatively affected mating success ($F_{1,79.22} = 28.91$; $P < 0.0001$) and positively affected the probability to behave aggressively ($F_{1,103.3} = 8.08$; $P = 0.005$).

DISCUSSION

Mating success appears to be critical in a European mink captive breeding program. For example, in 2010, only 40% of attempted males copulated with a female and in 2009, the percentage was 43. This study shows that breeding success is positively autocorrelated among breeding seasons, so a high proportion (67%) of males fail to pass their genes on to succeeding generations (64 of 96 males studied from 2004 to 2010). An inevitable outcome is a reduced genetic diversity in the population. The evidence accumulated from 1980 to 2003, when the European mink population at Tallinn Zoological Garden consisted of both captive born and wild born individuals, shows convincingly that mating failures were primarily attributable to captive born males. This suggests that the origin of the animals, rather than immediate environmental conditions during breeding attempts, is decisive in the minks' breeding performance. Indeed, in the related black-footed ferret (*Mustela nigripes*), it has been found that the behavior of the animals changes considerably between the first and all the following generations in captivity [Biggins, 2000]. Based on literature and our results, it appears reasonable to assume that growing up in a captive

TABLE 3. Generalized linear model for mating success (as binary variable) in captive European minks

	Full model			Reduced model		
Effect	ddf	*F*	*P*	ddf	*F*	*P*
Male						
Aggression index	81	25.31	<0.0001	92.73	24.68	<0.0001
Passivity index	81.48	63.90	<0.0001	87.35	63.95	<0.0001
Age	207.8	0.06	0.81			
Attempt	307.9	10.50	0.001	294.2	10.59	0.001
Female						
Experienced aggressiveness	115.8	13.07	0.0004	86.35	15.83	0.0001
Experienced passivity	101.9	10.35	0.002	84.15	9.04	0.004
Age	138.9	3.04	0.08			
Attempt	567	1.72	0.19	572	4.74	0.03
Earlier experienced aggressiveness	188.3	0.25	0.62			
Earlier experienced passivity	270	1.35	0.25			

The left column shows the full model, the right column is the reduced model containing statistically significant effects only. Female and male identities were included as random factors. See Table 1 for definitions of the variables, and descriptive statistics.

environment influences behavioral patterns in European minks and these changes in behavior are the likely reason for a low breeding success. However, as a number of captive born mink bred successfully, it is obvious that the origin alone is not the only determinant of (un)successful mating, but it is also a function of unknown factor(s) that the mink experience in captivity.

Detailed behavioral observations conducted from 2004 to 2010 allowed us to identify that, indeed, passivity and aggression in captive born males were the main reasons for failure in European mink breeding: (1) 24% of all failed mating attempts were judged as unsuccessful because of aggressive behavior in the male partner; (2) 47% of all mating attempts failed because of the male's passive behavior (i.e., a failure to be interested in the female). Aggressive or passive behavior in the male described far more variation in the outcome of mating events than did any other explanatory variables considered (e.g., age, previous experience of the female—see Table 1). In addition, our results suggest that passivity and aggression are two alternative expressions of the same phenomenon: the males' behavioral inability to mate. The males with a record of aggressive behavior were also more likely to behave passively in non-aggressive trials and vice versa. Similar to our findings, mating failures have also been identified as the cause of captive breeding problems in black-footed ferrets [Wolf et al., 2000]. Indeed, in the case of black-footed ferrets, the mating failure is, in addition to physiological disorders, also attributable to abnormal behavior. Males are either incapable of taking the proper mating position or they are aggressive toward females.

TABLE 4. Generalized linear model for mating success with male aggressiveness and passivity scored as binary variables

Effect	ddf	*F*	*P*
Aggressiveness (1/0)	82.97	9	0.0036
Passivity (1/0)	93.08	32.72	<0.0001
Experienced aggressiveness	453	15.54	<0.0001
Experienced passivity	453	18.47	<0.0001
Attempt (male)	453	8.06	0.0047
Attempt (female)	453	6.06	0.0142

Mating events having served as the basis of classifying males as aggressive or passive were omitted to avoid logical circularity.

Our results show that the outcome of a mating attempt depends largely on the male partner. The decisive role of male behavior in determining mating success has also been reported for southern lesser galagos (*Galago moholi*; Lipschitz et al., 2001] and for Giant pandas [Zhang et al., 2004]. However, some other studies have shown the opposite—the more important role of female behavior in defining mating success. For instance, Poole [1966] reports that the male European polecat (*Mustela putorius*) is aggressive towards a female only if the latter rejects her partner [Poole, 1966]. This does not hold for European mink, as males have repeatedly been observed to be aggressive towards female partner which is clearly interested in mating. Furthermore, our data do not allow us to conclude that the behavior of a male is altered with different female partners.

One of our hypotheses is that social stress [Blanchard et al., 2001] is a factor which causes the abnormal behavior of European mink raised in captivity. Indeed, the European mink is known to lead a solitary life style in the wild [Youngman, 1990]. However, in captivity, mink are usually accommodated in enclosures close to each other so that olfactory, visual and audio signals of the close presence of conspecific reach them all the time. This might cause stress resulting in distorted mating behavior. Such negative effects of social stress resulting in low mating success has been reported in captive wolverines, *Gulo gulo* [Dalerum et al., 2006], black rhinoceroses, *Diceros bicornis* [Carlstead et al., 1999], and various small felids [Mellen, 1991].

Besides creating social stress, the captive conditions may also influence an animal's behavior through the effects of size and environmental diversity of an enclosure. Indeed, it has been found that increasing the size and environmental enrichment of the cage positively affects the breeding success of giant pandas by raising the proportion of breeding events with normal mating behavior [Peng et al., 2007].

For European minks, no data are currently available to study immediate environmental factors associated with abnormal mating behavior, or those eliciting males' aggressive and passive behavior during breeding attempts. Nevertheless, a manipulative study is feasible here, as the sizes of the enclosures and their environmental diversity can be easily changed (e.g., we may change the enrichment and/or size of an enclosure and test whether or not there are any changes with relation to breeding behavior). Knowing that mating success primarily depends on male behavior and that the same males are behaving aggressively and passively allows us to properly identify target variables in such studies.

CONCLUSIONS

1. The negative effect of captive conditions on mating success in European Mink was much more expressed in captive born animals than in wild born animals: 89% of all captive born males failed in breeding in contrast to 35% of wild born males.
2. Abnormal mating behavior was the strongest predictor of breeding failure in captivity. Twenty-four percent of all recorded failures in mating were associated with aggressiveness and 47% with passiveness.
3. Mating success, as well as aggressiveness and passivity, were all shown to depend much more strongly on the male than on the female partner.
4. No evidence was found that the behavior of an individual was dependent on the identity of its partner.
5. Passivity and aggressiveness are suggested to be two alternative expressions of the males' behavioral inability to mate. The aggressive males tended to behave passively in non-aggressive situations, and vice versa.

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