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Reproduction in mustelids

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Abstract

This paper is an attempt to review in a comprehensive manner the reproduction in Mustelidae, based mainly on our own experience of breeding and investigating in captivity various Mustelidae species, mostly of European and Asian origin. Literature data on reproduction in other Mustelidae species used as reference.

Keywords: Mustelids; Reproduction; Embryo development; Delayed implantation

1. Introduction

There are about 70 extant Mustelidae species (Ternovsky and Ternovskaya, 1994). Some of them are used as pelt producers and sometimes as pets and pest killers. Besides, the majority of mustelids have a great aesthetic value for man. The colour, shades and texture of their fur and the gracefulness and beauty of their movements have a strong favourable influence on human emotions. American mink (*Mustela vison*) was adapted to ranch rearing at the beginning of this century, and nowadays this species has the highest economic value among mustelids as a fur producer. Sable (*Martes zibellina*) was introduced into farming more recently and is used as a farm animal almost exclusively in Russia. The third Mustelidae species, which is used as a farm-bred fur bearer is the European polecat (*Mustela putorius*). An albino form of European polecat, known as the domestic ferret (*Mustela putorius furo*) has a long history of domestication, and there are evidences of this history. Most of the Russian fur animal experts agree that the animal figuring in the masterpiece ‘‘Lady with a stoat’’ is in fact not a stoat but a

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Table 1
Reproductive characteristics of 11 Mustelidae species bred in captivity
Referenced from Ternovskaya (1983), Ternovsky and Ternovskaya (1994), Amstislavsky et al. (1993, 1999) and our unpublished experiments done in the Experimental Research Station in Novosibirsk, Russia.
In the case of sable twice mating system (mating for two consecutive days) was used.

Species (number of litter obtained at the Research Station)	Breeding season	Peak of breeding activity	Pregnancy length M ± m (range)	Litter size M ± m (range)	Reproductive peculiarities, discovered or confirmed at the Research Station
American mink — *M. vison* (38)	Late February–March	March	52.3 ± 0.72 (45–61)	5.4 ± 0.35 (1–10)	Males of *M. vison* may impregnate *M. lutreola* females, but resorption occurs at late stage of pregnancy
European mink — *M. lutreola* (274)	Late March–June	April	41.6 ± 0.08 (39–44)	4.6 ± 0.09 (1–9)	Interspecies hybrids with *M. putorius*, *M. putorius furo*, *M. eversmanni*, and *M. sibirica* were obtained
European polecat — *M. putorius* (14)	April–early August	April	40.3 ± 0.12 (40–41)	5.8 ± 0.82 (1–11)	Interspecies hybrids with *M. lutreola*, *M. putorius furo*, *M. eversmanni*, and *M. sibirica* were obtained
Domestic ferret — *M. putorius furo* (28)	Late March–August	April	41.0 ± 0.17 (39–42)	8.6 ± 0.62 (1–15)	(1) Interspecies hybrids with *M. putorius*, *M. lutreola*, *M. eversmanni*, and *M. sibirica* were obtained (2) Successful embryo transfer from *M. putorius furo* to *M. putorius*
Steppe polecat — *M. eversmanni* (32)	March–May	March–April	38.1 ± 0.02 (37–39)	8.6 ± 0.63 (1–17)	Interspecies hybrids with *M. putorius*, *M. lutreola*, *M putorius furo*, and *M. sibirica* were obtained

Sable — *Martes zibellina* (543)[a]	June–July	Early July	278.6 ± 0.79 (261–297)	2.2 ± 0.08 (1–7)	Late sexual maturity of both sexes was confirmed
European pine marten — *Martes martes* (5)	July	July	271.3 ± 2.36 (265–279)	3.4 ± 0.24 (1–4)	Possibility of successful captive breeding was confirmed
Stoat — *M. erminea* (adults) (38)	April–September	June–July	298.0 ± 4.99 (240–371)	6.4 ± 0.59 (1–14)	Different duration of copulation of the adult males during mating to young or adult females
Stoat — *M. erminea* (young females (58)	Late April–August	May–June	317.9 ± 3.64 (224–393)	7.4 ± 0.45 (1–14)	Extremely early sexual maturation of females at the age since 20 days was confirmed
Siberian weasel — *M. sibirica* (30)	April–August	Late April	33.5 ± 0.15 (32–35)	6.2 ± 0.49 (2–12)	Interspecies hybrids with *M. putorius*, *M. lutreola*, and *M putorius furo* were obtained
Mountain weasel — *M. altaica* (97)	Late February–May	March	39.1 ± 0.12 (37–42)	8.7 ± 0.38 (3–14)	Possibility to reproduce in captivity
Least weasel — *M. nivalis* (3)	May–September	June	34	6	

[a]Reproductive data in all species except sable were obtained in our Research Station with the use of single mating system. Data on sable have been obtained not only at this station, but also in a more earlier work of Ternovskaya (1983) in Pushkin’ and Lesnoi’ fur farms.

domestic ferret. The current opinion is that this picture was created by Leonardo da Vinci in 1482–1485 (Rzepinska, 1978).

Domestication has significantly changed the reproduction of ferret. This may be illustrated by comparison of reproductive characteristics of the European polecat (*M. putorius*) with its albino domesticated form (Table 1). Except for the domestic ferret, no Mustelidae species may be considered as domesticated. Nevertheless, all these Mustelidae species (American mink, sable, and European polecat) have been bred for fur quality and ability to reproduce successfully in captivity. The history of farming of sable is very illustrative in this respect. The fur quality of the farm-bred sable is much better than that of its wild counterpart (Pavljuchenko et al., 1979). Moreover, sables with different types of behaviour have different reproductive success in farms (Ternovskaya, 1983).

American mink and ferret reared in captivity have been intensively used for research for about a century. The reproduction of the sable has also been thoroughly studied, especially in Russia (see Manteifel, 1934; Ternovskaya, 1983 for review). Physiology of the reproduction of other mustelids is less well known (Mead, 1989). In total, 11 different Mustelidae species have been successfully bred in captivity and studied for a number of generations at the Research Station in Novosibirsk (Russia) founded by Dmitry Ternovsky in 1967 (Table 1). Experimental data on these species, which rarely if ever bred in captivity, are discussed below. The American mink, whose reproduction has been thoroughly studied world wide was used as the ‘‘reference’’ species.

2. Sexual maturation in mustelids

Most of the Mustelidae species become sexually mature within 8–12 months after birth. But some exceptions exist. Young stoat females studied at our Research Station became sexually attractive for adult males and conceived at an age of 20 days (Ternovsky, 1977; Amstislavsky et al., 1993; and our unpublished observations). This extremely precocious sexual maturation of females long before they are physically mature is a specific feature of this species. Due to delayed implantation, stoat females deliver offspring the next year, after they become physically mature. In some other species, such as the long-tailed weasel (*Mustela frenata*), the least weasel (*Mustela nivalis*), the Western spotted skunk (*Spilogale gracilis*), and the American badger (*Taxidea taxus*), early sexual maturity of females, at the age of 3–5 months, has been recorded as well (see Mead, 1989 for review). In contrast to females, early maturation in males has never been observed, at least not in the species bred at our Research Station (see Table 1). Some Mustelidae species begin to reproduce relatively late. It was confirmed in our previous work (Ternovskaya, 1983), that only about 20% of sables reproduce at the age of 15 months, but most of them begin breeding only at the age of 27 months. The river otter (*Lutra canadensis*) and the American pine marten (*Martes americana*) do not breed until they reach an age of 2 years (Mead, 1989). It has been shown that some reproductive characteristics of females, such as reproduction success in captivity in the American mink and sable (Ternovskaya, 1983; Elofson et al., 1989) and the total length of pregnancy in captive bred stoats (Ternovsky and Ternovskaya, 1994) strongly depend on the age.

3. Breeding of mustelids: oestrus, mating, and ovulation

A large majority of Mustelidae species are reflex ovulators, and a coital stimulus is required to trigger the ovulation (Mead, 1989). Nevertheless in some Mustelidae species, such as the American mink, corpora lutea have been found sometimes in ovaries of unmated females indicating that ovulation might occur in this species spontaneously under some conditions (Moller, 1974; Gustaffson et al., 1987). In ferrets, preintromission events do not lead to any increase in ovulatory hormones and do not induce ovulation (Carroll et al., 1985). In contrast, ovulation in American mink may result from a contact with a male, not necessarily involving intromission (Enders, 1952). The duration of the copulatory act varies significantly across individual animals within the species. We observed that in the stoat, the duration of the copulatory act was usually about 15 min, but sometimes varied from 1 min to about 1 h. Even more pronounced variations have been observed in the domestic ferret and American mink (Carroll et al., 1985; Ternovsky and Ternovskaya, 1994). The duration of the copulatory act in American mink depended also on the date of mating during the breeding season (Elofson et al., 1989).

Sexual behaviour differs markedly across Mustelidae species. A stud stoat male copulates with young female in oestrus almost immediately after they are brought together. On the other hand, an adult sexually mature female European mink or sable, when in oestrus, may reject the stud male, even if he is sexually mature and eager to copulate. But the same female may immediately mate with another male.

We investigated mating-induced ovulation in the stoat (Amstislavsky et al., 1993; and later unpublished observations). Fresh ovulation sites in the ovaries and ovulated oocytes in the oviducts were observed in this species 72–96 hours post coitum. In American mink, the interval between copulation and ovulation varies within a range of 33–72 h (Hansson, 1947; Enders, 1952). Copulation is accompanied in female mustelids by a rise of luteinising hormone (Carroll et al., 1985), which causes ovulation. The relatively long period between copulation and ovulation seems to be associated in mustelids with a prolonged period of sperm survival in the reproductive tracts of females. We have flushed mobile spermatozoa from the reproductive tracts of stoat females during 96 h after copulation (Amstislavsky et al., 1993). Chang (1965) demonstrated that in the ferret, spermatozoa retained their fertilising capacity in the female reproductive tracts during 120 h. The time of sperm survival in mustelids is thus much longer as compared to a large majority of other mammals (Johnston and Everitt, 1995), and this may be closely associated with the evolution of mustelids as reflex ovulators.

The majority of Mustelidae species in the Northern hemisphere are seasonal breeders. Species with short pregnancy such as minks, polecats, and some weasel species start their breeding season in early spring or even in February with the peak of breeding activity observed in March–April. Species with prolonged pregnancy accompanied by delayed implantation such as sables, martens, and stoats start their breeding in summer or spring, but usually the peak of their breeding activity occurs in mid-summer (see Table 1). Out of breeding season mustelids of opposite sexes, being paired in captivity, do not mate, but interact sometimes in an aggressive manner, with a great danger to their lives.

Most wildlife Mustelidae species in the Northern hemisphere are either monooestrous or seasonally polyoestrous (Mead, 1989). This pattern of reproductive activity is retained also in captivity, but the duration and frequency of oestrus differ markedly across species. We observed, that in the European mink (*Mustela lutreola*), the duration of the oestrus period is 1–10 days, wherein oestrus in unmated females may recur two to three times during the breeding season. Formally, the European mink is a seasonally polyoestrous species. On the other hand, all stoat females bred at our station exhibited oestrus only once a year, but once the oestrus had set on, it lasted for a long period of time (sometimes, 2–3 months), until it was terminated by mating with a male. This species is formally monooestrous. The large-scale experiments on the American mink (*M. vison*) performed in Uppsala (Sweden) have demonstrated that oestrus in captive-bred American mink is more similar to that of the stoat, than to that of European mink. These studies (Elofson et al., 1989) clearly indicate that once a female American mink has come into oestrus, she is receptive at any time during the mating season.

In all Mustelidae species listed in Table 1, a single mating with intromission was enough to induce ovulation in most of the females. Thus, our observation is in agreement with that of Carroll et al. (1985). Nevertheless, mink and sable breeders in commercial fur farms usually remate females to maximise reproductive output (Ternovskaya, 1983).

Though different Mustelidae species are usually formally classified as either mono or seasonally polyoestrous, they have more similarities than dissimilarities. In the Northern hemisphere, it is the day length that determines the beginning of the breeding season in most of Mustelidae species. Moreover, folliculogenesis is active in the ovaries of Mustelidae females during all the period of oestrus, which sometimes comprises a relatively long time. We observed well-differentiated antral follicles 0.5–0.6 mm in diameter in the ovaries of the stoat throughout the breeding season. Ovaries of unmated American mink females in oestrus resemble those of the stoats. Moreover, folliculogenesis is active in mated minks also during the first weeks after mating (Douglas et al., 1994). In American mink, if unmated, follicles may undergo luteinisation without ovulation, or degeneration at the end of the breeding season (Lagerkvist et al., 1992).

4. Pregnancy, embryo development and delayed implantation

Three principal types of pregnancy have been identified in Mustelidae species (Ternovsky, 1977; Mead, 1989). Such species as the European mink, all polecat species, as well as the least weasel (*M. nivalis*), the mountain weasel (*Mustela altaica*), and the Siberian weasel (*Mustela sibirica*), have all a relatively short period of pregnancy of constant duration; the shortest gestation length was observed in the least weasel and the Siberian weasel (see Table 1). The gestation length of some other Mustelidae species which have never been bred at our station was also considered as short and constant (Mead, 1989). This type of gestation may be illustrated on European polecat (Amstislavsky et al., 1999). The period of ovulation together with the oviductal journey of cleavage stage embryos in this species comprises about 5–6 days. After migration into the uterus and expansion, blastocysts get implanted (without delay of implantation) mainly on Day

12–13. The post-implantation period of development comprises an additional 27–28 days.

In the stoat, the sable, the European pine marten, and the Western spotted skunk (*Spilogale putorius latifrons*) embryo development includes an obligatory diapause at the blastocyst stage, and the gestation encompasses a longer period (7–10 months). The peak of the breeding season in these species occurs usually in summer, and offspring appear in the next spring. Additionally, to the species listed in the Table 1, this type of pregnancy has been described in a large number of other Mustelidae species (Mead, 1989). The stoat may be an illustrative example of this type of gestation (Deanesly, 1943; Ternovsky, 1977; Amstislavsky et al., 1993). The period of implantation delay and embryonic diapause encompassed about 9 months in this species. During this period of dormancy, the blastocysts of the stoat and other mustelides with obligate embryonic diapause undergo a gradual increase in size and achieve a diameter of about 1 mm and even more. This is accompanied by increased fluid accumulation within the blastocoel and an increase in embryonic cell numbers. But very few morphological changes are observed in the cells except an arrest of differentiation in the inner cell mass (Baevsky, 1955; Enders et al. 1986; Amstislavsky et al., 1993). The differentiation process in the stoat, the sable, and the Western spotted skunk resume closely before implantation and a distinctly separated population of cells could be distinguished on the surface of the inner cell mass (Baevsky, 1955; Enders et al., 1986; and our unpublished observations). It has been shown that blastocysts of skunk (Enders et al., 1986) expand rapidly during the last 24–48 h prior to implantation and achieve a size of 2 mm.

The American mink and the stripped skunk (*Mephitis mephitis*) represent the third type of pregnancy — the gestation period is relatively short and variable. In the American mink implantation (lasting from 0 to 40 days) may or may not be delayed depending on the date of mating (Mead, 1989). It should be noted that, despite the similarity in denomination and in the occupied ecological niche, the reproductive physiology of the American mink and the European mink differs considerably. For example: delay of implantation is present in the former and absent in the latter. Breeding season, pregnancy lengths, and some other reproductive features differ in these species (Ternovsky, 1977; Maran and Henttonen, 1995).

It has been shown that it is possible to obtain, in captivity, interspecies hybrids between Mustelidae species with short and constant gestation periods (see Table 1). The interspecies hybrids between the European mink and the European polecat occur sometimes in nature (Ternovsky, 1977). This type of hybridization has been used on a large scale at our Research Station with a high economic profit (Ternovsky, 1977; Ternovsky and Ternovskaya, 1994).

5. Endocrinological aspects of reproduction in mustelids

We observed that corpora lutea were inactive during the period of delayed implantation in stoats (our unpublished observations). Gulamhusein and Thawley (1974) revealed that lack of luteal activity in the ovaries during the period of diapause corresponded to an extremely low plasma progesterone level during the whole period of delayed implantation. Plasma progesterone levels do not differ significantly in pregnant and non-pregnant female stoats from June to January. The highest level of plasma progesterone observed in pregnant stoats in February–March (Gulamhusein and Thawley, 1974) preceded implantation which occurs in this species at the very beginning of April (our unpublished observations).

The endocrinological aspects of delayed implantation have been thoroughly investigated in farmed American mink (Stoufflet et al., 1989; Lagerkvist et al., 1992). The progesterone concentration in plasma remains low in female minks until late March, but then gradually increases. This increase of progesterone concentration does not depend on the date of mating, but correlates with corpus luteum activation. In the American mink, the growth of the corpora lutea began by a cellular hypertrophy (Moller, 1973). The increase in cell size is followed in this Mustelidae species by an increase in luteal cell number (Stoufflet et al., 1989). This process results in a significant increase in luteal tissue weight at the time of implantation (Stoufflet et al., 1989). Implantation occurs in the American mink at the beginning of April, and this corresponds to the highest plasma progesterone level.

Taken together, experimental data strongly suggest that in diapausing Mustelidae species, the photoperiod dictates an increase of plasma progesterone level and thereby induces the implantation. The arrest of embryo development during the diapause in mustelids is thought to be a consequence of inability of the corpora lutea to secrete enough progesterone. This conclusion has been confirmed experimentally. It was shown that passive immunization with anti-progesterone monoclonal antibodies arrested normal embryo development in ferrets (Rider and Heap, 1986). Some kind of ‘‘artificial diapause’’ was observed in this species after such a treatment. On the other hand, termination of the diapause in mink was associated with increased prolactin secretion (Murphy et al., 1981). Successful in vitro culture of American mink embryos in different co-culture systems resulted in reinitiated development of some diapausing embryos (Moreau et al., 1995). This study created a positive background for elucidation of the whole chain between photoperiodic signals and resumption of embryonic development in diapausing Mustelidae species.

Plasma oestradiol concentration in American mink females as well as testosterone concentration in males increased gradually before the breeding season (Gulevich et al., 1995). Plasma oestrogen level in this species was significantly higher in March than in January. An additional increase of plasma oestradiol concentration associated with embryo implantation was observed in female minks at the beginning of April (Lagerkvist et al., 1992). A thorough endocrinological study of sable revealed a sharp peak of plasma oestradiol two days before mating (Polinzev et al., 1975).

6. Peculiarities of reproduction in mustelids

This brief description highlights some peculiar features of reproduction in mustelids. The large majority of mustelids are seasonal photosensitive breeders. The breeding season of most Mustelidae species in the Northern hemisphere is restricted to a relatively well defined period lasting no more than 3–4 months. This period of breeding activity is followed by a long period of sexual rest, sometimes accompanied by a significant gonadal regression in males.

It should be noted that the post-implantation period is about 23–31 days in the majority of Mustelidae species (except badgers, wolverine, and river otter), but the duration of the gestation period may vary within a broad range in diapausing species. The duration of implantation delay and the date of implantation strongly depend on the photoperiod in the large majority of Mustelidae species.

Another feature common to all Mustelidae species is the relatively large size of embryos. The diameter of blastocysts in the American mink (Stoufflet et al., 1989) and the spotted skunk (Enders et al., 1986) is about 2 mm at implantation. This is not a consequence of the implantation delay, because large blastocysts have been observed in polecats as well, though there is no implantation delay in these species (Amstislavsky et al., 1999). Despite the large size, the embryos of Mustelidae animals may freely migrate from one uterine horn to another.

Preimplantation embryos of different Mustelidae species contain more lipid droplets when compared to most laboratory and farm animals (Hansson, 1947; Baevsky, 1955; Enders et al. 1986; Gustaffson et al., 1987; Amstislavsky et al., 1993; Kizilova et al., 1998). The specific dark color of Mustelidae embryos is due to a large number of lipid droplets in the blastomeres. This is a characteristic feature not only of Mustelidae embryos, but also of embryos of other Carnivora mammals.

Mustelids demonstrate some reproduction peculiarities, which are sometimes curious, such as the lack of prostate gland in male ferrets (Canadian Council on Animal Care, 1984). The stoat, which is one of the most surprising Mustelidae species, exhibits two ‘‘reproductive miracles’’: an extremely precocious sexual maturation of females long before weaning and an amazingly prolonged (about 9 months) period of delayed implantation. These are the peculiarities that have led to the unusual pattern of reproduction in the stoat, which includes impregnation of females in the early childhood by adult males (Gulamhusein and Thawley, 1974; Ternovsky, 1977; Amstislavsky et al., 1993).

7. Conclusion

Mustelids are polytocous Carnivora species demonstrating a pronounced variety of reproduction characteristics. With some exceptions, mustelids may be characterised as reflex ovulators. In the Northern hemisphere, most Mustelidae species breed in a restricted and usually well defined period during the late winter and spring or in summer, but in some species the breeding season continues till autumn. Implantation delay and obligate embryonic diapause are characteristics of many Mustelidae species. Photoperiod usually determines the beginning of the breeding season, timing of embryo development, and implantation. Reproduction of the American mink, the ferret, and a few numbers of other Mustelidae species have been thoroughly investigated. More reproductive data need to be obtained in other mustelids, which are not normally bred in captivity, but may be of great scientific interest.

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