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Environmental Factors and Reproduction in Farmed Blue Fox (*Vulpes lagopus*) Vixens

Doctoral dissertation

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ABSTRACT

The highest possible reproductive success is one of the main goals in animal production and forms the basis for economically profitable animal production. Reproductive success can also be used as a measure of welfare, since unpleasant stress may impair reproduction. Reduced reproductive efficiency can be the result of environmental factors or stressors associated with animal housing, human-animal relations and management. Barren housing environment in farmed blue foxes (*Vulpes lagopus*), has been claimed to cause reduced reproduction and abnormal behaviour, such as maternal infanticide.

The present thesis evaluated maternal behaviour and the incidence of maternal infanticide in farmed blue fox vixens during both whelping and exposures to aviation noise. In addition, the effect of acute stressors, i.e., aviation noise and handling, on behaviour and deep body temperature were of particular interest. The reproductive performance (RPM, i.e., cubs per mated vixen) of alternative housing solutions was compared with that of traditional housing. The solutions included changes either in foxes' social environment (pair-housing, stable social environment, low housing density), physical environment (a top and tunnel nest, two nests) or both. The main idea underlying the experimental design was that if the traditional breeding conditions have adverse effects on foxes' welfare, positive changes in their housing environment should enhance RPM.

Proper maternal behaviour was exhibited by both the primiparous and the multiparous vixens before, during and after whelping, despite moderate cub losses. The primiparous vixens were probably more restless than the multiparous vixens, as shown by the less amount of time spent inside the nest. The present results indicate that there are no major behavioural problems arising due to present farming conditions during the breeding season. It is also possible that infanticidal behaviour is not included in the reproductive strategies of *V. lagopus*. In that case, the lack of infanticidal behaviour still indicates that blue fox vixens on farms are, in spite of the barren environment, able to follow their natural behavioural patterns in cub care. Changes in social or physical housing environment had no clear effect on RPM or its subcomponents (percentage of vixens without oestrous, barren vixens, and vixens that weaned cubs, litter size and cub losses). On the other hand, RPM seemed to be more affected by management than the studied alternative housing solutions. To improve the welfare and RPM of farmed blue fox vixens, more attention should be focused on human-animal relations, management procedures (e.g., feeding, breeding animal selection, farming routines) and co-operation between research and practice.

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ABBREVIATIONS

ACTH	Adrenocorticotropin
AI	Artificial insemination
BLUP	Best linear unbiased prediction
CRH	Corticoliberin
EC	European Convention
EU	European Union
EXPOd	The day of acute stressors, i.e., aviation noise or handling
EXPO-1d	The day before exposure to acute stressors
EXPO+1d	The day after exposure to acute stressors
EXPO	The period of exposure to acute stressors
EXPO-1h	Hour before exposure to acute stressors
EXPO+1h	Hour after exposure to acute stressors
FAWC	Farm Animal Welfare Council
FFBA	Finnish Fur Breeders' Association
GLM	General linear model
HAR	Human animal relationship
HD	High animal density
HPA	Hypothalamic-pituitary-adrenal
IS	Instantaneous sampling
LD	Low animal density
NB	Natural breeding
PC	Pair-housing in cage environment
PE	Pair-housing in an enclosure
RPB	Number of cubs per breeding female
RPM	Number of cubs per mated female
SC	Single-housing in cage environment
SIH	Stress-induced hyperthermia
SSE	Stable social environment
T_b	Deep body temperature

LIST OF ORIGINAL PUBLICATIONS

This dissertation includes the following papers referred to in the text by their Roman numerals I-V:

I   Pyykönen Teija, Mononen Jaakko, Ahola Leena, Rekilä Teppo: Periparturient behaviour in farmed blue foxes (*Alopex lagopus*). Applied Animal Behaviour Science 94: 133-147, 2005

II   Pyykönen Teija, Hänninen Sari, Mohaibes Maarit, Sepponen Juhani, Mononen Jaakko, Ahola Leena: The effect of a combination of permanent breeding cage and low housing density on the reproductive success of farmed blue foxes. Animal Reproduction Science 106: 255-264, 2008

III   Pyykönen Teija, Ahola Leena, Mononen Jaakko: A note on the reproductive success of primiparous blue fox vixens in social groups. Animal Reproduction Science (2008), doi:10.1016/j.anireprosci.2008.05.010

IV   Pyykönen Teija, Ahola Leena, Mononen Jaakko: Effect of an additional nest on reproduction in breeding blue fox vixens: a preliminary study. Submitted to Animal Welfare

V   Pyykönen Teija, Juntunen Jyrki, Ahola Leena, Parri Asko, Mononen Jaakko: Aviation noise does not impair the reproductive success of farmed blue foxes. Animal Reproduction Science 97: 128-136, 2007

This thesis also contains previously unpublished data. Unpublished data from the experiments presented in III and V are based on the material and methods of the original publications and marked with superscript [u] (i.e., III[u], V[u]).

1.   INTRODUCTION

In the wild, an individual animal tries to leave as much reproducing offspring as possible and reach the highest possible inclusive fitness (Alcock 1997). Inclusive fitness is the sum of direct and indirect fitness, which are measured in terms of personal reproductive output and of genetic gains derived by helping relatives. Therefore, inclusive fitness represents the total genetic contribution of an individual to the next generation.

As in the wild, in animal production one of the main goals is to reach the highest possible reproductive success in terms of numbers of healthy offspring produced. In fur animal production, high reproductive performance has been the main target for selection in addition to high fur quality. The reproductive performance of farmed blue foxes (*Vulpes lagopus*) has, however, decreased over the last decades in Finland (Finnish Fur Breeders' Association, FFBA 2007ab, Peura and Stranden 2003). Impaired reproductive performance may be the consequence of selecting for large body size (Peura and Stranden 2003, Peura et al 2004a), or it may reflect the negative effects of unsatisfactory management (farmed foxes: Sanson and Farstad 2003) or inappropriate housing conditions (Broom and Johnson 1993, farmed foxes: see, e.g., Bakken et al 1994, Nimon and Broom 2001). It has even been proposed that the present barren housing conditions in which farmed foxes live in could induce abnormal behaviour, such as maternal infanticide (Nimon and Broom 2001).

Living conditions may indeed have an effect on reproduction through stress mechanisms (e.g., Broom and Johnson 1993, Moberg 2000). Stress, defined as a biological response elicited when an animal perceives a threat to its homeostasis, may induce changes in the secretion of pituitary hormones (Moberg 2000), thus leading to altered metabolism, immune competence and behaviour, as well as failures in reproduction if the biological costs of a stress response are greater than the biological reserves needed to satisfy these costs. In other words, resources are shifted from other biological functions to the stress response, thereby impairing these other functions. Thus, stressful conditions could also diminish reproductive success. Therefore, reproductive performance and reproductive failures can be used as one of several measures of animal welfare. Others are e.g., abnormal behaviour, e.g., infanticide, abandoning of cubs and excessive mothering, elevated levels of stress hormones in

blood as well as morbidity and mortality (Broom and Johnson 1993). The welfare of animal is good if it is free from thirst, hunger, malnutrition, discomfort, pain, injury, disease and other negative states and experiences comfort, pleasure and other positive stimuli to avoid boredom and inactivity (so called Five Freedoms, see e.g., Duncan and Fraser 1997).

Good reproductive performance and animal welfare form the basis for economically profitable animal production. The welfare of farmed foxes could be enhanced through the development of foxes' housing conditions and breeding methods based on research. This, in turn, could improve the reproductive performance, and concurrently increase the economic benefits of blue fox production. Thus, improving the housing conditions benefits both the farmers and the foxes.

The present thesis aims to elucidate the factors affecting reproduction in farmed blue fox vixens by describing maternal behaviour by assessing the incidence of infanticide during the whelping period, and by studying the effects of acute stressors, social environment, nest design and location, and alternative management procedures on reproductive success and welfare.

2.   LITERATURE REVIEW

2.1 Arctic fox in the wild

2.1.1 General

Arctic fox (*Vulpes lagopus*) is the smallest (3-5 kg) homeothermic carnivore (canid) that remains active in the Arctic during the winter (Prestrud 1991). It inhabits a variety of coastal, inland, alpine, and marine habitats and occupies areas with the best possible food supplies (Stickney 1991). Arctic foxes are predators and scavengers (Kennedy 1980, Garrott et al 1983a, Anthony 2000). They rely on small mammals, such as lemmings (*Dicrostonyx, Lemmus*) and voles (*Microtus*), but may also consume birds, eggs, marine invertebrates, fish and the carcasses of sea mammals when rodents are rare or absent. The wild arctic fox has adapted well to an extreme environment with fluctuating food resources, in which it is essential to assimilate the energy available as efficiently as possible (Fuglei et al 2004). Thus, the seasonal variation in body fat and body weight is high, since arctic foxes have a great capability to gather extensive adipose tissue stores in the autumn. Deposition of subcutaneous and visceral fat occurs in August-September, with the maximum fat content being reached in November-December, when the body lipid stores may constitute over 20 % of the total body weight (Prestrud 1991, Fuglei et al 2004).

2.1.2 Breeding ecology

Age at maturity, the proportion and age structure of reproducing females, number of litters per season, and average litter size are important components of the reproductive rate of most mammals at the population level (Millar 1977). In populations of the arctic fox, litter size and the proportion of reproducing females have been found to be the main determinants of reproductive rate (Macpherson 1969, Bannikov 1970, Prestrud 1992a, Angerbjörn et al 1995). Those populations living in distinct habitats, i.e., near ice-free coasts or inlands, show marked differences in their food availability, thus leading to the development of two different reproductive strategies (Frafjord 1993a, Tannerfeldt and Angerbjörn 1998). Foxes living near ice-free coasts have access to both inland and marine prey, resulting in relatively stable food availability and a more

generalist feeding strategy. Coastal foxes with a stable food supply have a high probability of future reproduction (Frafjord 1993a) but produce relatively few cubs (average 4-6) (Bannikov 1970, Frafjord 1993a, Tannerfeldt and Angerbjörn 1998). Inland foxes, by contrast, are usually specialists or semi-generalists relying on fluctuating microtine rodent populations (Prestrud 1992a, Hersteinsson and Macdonald 1996). Although inland foxes have larger litter sizes (average 8-12) than costal foxes, they may reproduce only once in a lifetime, during the peak of small rodents (Chirkova et al 1959, Macpherson 1969, Frafjord 1993a). In those cases characterised by fluctuating environmental conditions, selection pressure is put on increased litter size in species with individuals having a lifespan similar to the interval of environmental fluctuations (Tuljapurkar 1985). Such appears to be the case in arctic fox populations, at least in Scandinavia (Angerbjörn et al 1995). Under favourable conditions during lemming peaks, large litters of up to 20 - 22 cubs may occur (Chirkova et al 1959). On the other hand, during years when food is scarce, the average number of kits in a litter can be as low as 3-5 cubs. Within both strategies, variation can also exist in litter size, due to regional changes in food abundance, which affects prenatal mortality and cub survival (Angerbjörn et al 1995, Strand et al 1999, see also a review by Tannerfeldt and Angerbjörn 1998).

Although arctic foxes are mainly non-social, a male and a female can share and defend a territory during the reproductive season (Eberhardt et al 1983). Accordingly, arctic foxes are basically monogamous. Sometimes, supplemental adults are, however, observed at the denning area (Eberhardt et al 1983, Frafjord 1984, 1991, Hersteinsson 1984). These non-breeding foxes are believed to be previous progeny of the breeding pair.

Arctic foxes are monoestrous, seasonal breeders with spontaneous ovulation, lasting 4-5 days (Audet et al 2002). Reproductive activity occurs only during late winter and spring from February to May. Increasing daylight in the spring months triggers the onset of follicular development and oestrus, and foxes are therefore characterized as long-day breeders. However, decreasing daylight during the autumn primes the hormonal changes responsible for spermatogenesis and development of the ovaries and oestrus in the spring (Farstad 1992). Mating occurs in March – April, depending of the latitude, weather conditions and physical condition of the foxes (Audet et al 2002). Gestation

lasts ca. 52 days, with the cubs being born altricial. Their eyes and ears start to function at 14-16 days postpartum. New-born cubs can hardly move but succeed in finding a nipple. Cubs emerge from the dens after 3-4 weeks. They are weaned at the age of 6-8 weeks and become independent at the age of 12-14 weeks (Garrot et al 1984, Garrot and Eberhardt 1987). The cubs disperse at the age of 6-10 months. Some of the cubs may return to their home range and act as auxiliary individuals in later years (Strand et al 2000).

For whelping, arctic foxes prefer certain dens, which they tend to use season-after-season to rear young. Other dens are used infrequently and only during times of high densities of foxes (Eberhard et al 1983). The vixens whelp in underground dens excavated at the crests of slopes, on banks, or on mounds with an unrestricted view over the denning area (Chesemore 1969, Garrot et al 1983b, Garrot and Eberhardt 1987, Prestrud 1992bc, Szor et al 2008) often with southern exposures (Prestrud 1992c, Audet et al 2002, Angerbjörn et al 2004, Szor et al 2008). Such locations have deeper unfrozen soil layer over permafrost and a lower level of ground water (Szor et al 2008). Though sometimes consisting of single burrows, the dens more often comprise large, complex structures (Garrot et al 1983b, Garrott and Eberhardt 1987 Dalerum et al 2002). A den may cover over 50m^2 with up to 100 entrance tunnels, on average 34 cm in diameter (Chesemore 1969, MacPherson 1969, Prestrud 1992b).

Arctic foxes may have multiple dens in use during a breeding season (Eberhardt et al 1983, Frafjord 1991, 1992a). Generally, only a portion rather than the entire litter is moved to another den (Eberhardt et al 1983, Frafjord 1992ab). These transfers are common from early to mid July when the young are 5-7 weeks old. After the initial move, cubs may be interchanged between dens several times (Eberhardt et al 1983). Transferring cubs and splitting litters in several dens may reduce the chance of losing an entire litter to predation (Garrot and Eberhardt 1982), and reduce the potential for disease transmission by decreasing the contacts between siblings (Eberhardt et al 1983).

Natal dens are abandoned by cubs at the age of 6-12 weeks (Fine 1980, Garrott et al 1984, Frafjord 1992a). The abandoning age may be advanced due to unsatisfactory food resources or the presence of predators (Garrot and Eberhardt 1982, Frafjord et al 1989,

Frafjord 1992a). Cubs may move into an area with a better food supply, split up into several dens, or follow adults without returning to any particular den (Frafjord 1992a).

2.1.3 Parental behaviour and cub care

Little is known about early events in the life of arctic fox cubs due to the difficulty of observing new-borns and their mothers in underground dens. Nevertheless, reproducing vixens are known to stay close to the newborns and are rarely seen outside the den until the emergence of cubs, on average, at three weeks of age (Frafjord 1991). During these first three weeks, the male brings food to the female. After the emergence of the cubs from the dens, the male also plays with the young. As cubs grow older, the female substantially reduces her time at the den. Generally, both parents bring food to the young at about equal frequency (Garrot et al 1984, Frafjord 1991). The male and the female hunt and rest alone and seldom interact (Frafjord 1991). Adult foxes at dens are inactive 60-90 % of the cub-rearing period. After cubs' emergence from the den, the cubs soon become more active and more frequently follow the adults. Because the female spends more time with the cubs, she also chases away cubs more frequently than the male, which in turn more easily retreats away from the den. Adult aggression towards cubs is restricted to avoidance of cubs, i.e., keeping them at a distance.

In canids, the reproductive strategy often involves efforts in helping, i.e., increasing the reproductive success of relatives (see a review by Geffen et al 1996). Such helping behaviour may increase the inclusive fitness of the helper in two different ways. The so-called primary helpers contribute significantly to parental care (i.e., provide the offspring of close relatives with food or safety against predators), and raise their own fitness indirectly through the increased production of relatives (Alcock 1997). By contrast, secondary helpers raise their fitness directly by increasing their own future chances to reproduce (Alcock 1997), e.g., by gaining experience in the caring of cubs or by inheriting the parents' breeding territory (Lindström 1986).

In arctic foxes, the role of helpers is unclear. It appears that helping occurs among arctic foxes less infrequently than expected for their large litter size (Hersteinsson and Macdonald 1982, Frafjord 1991). Supplemental adults, which are believed to be the progeny of the breeding pair, are nevertheless sometimes found at arctic fox dens

(Eberhardt et al 1983, Frafjord 1984, Garrot et al 1984, Hersteinsson 1984). Surplus females generally emigrate from the denning area before cubs become independent from the den (Hersteinsson and Macdonald 1982). Surplus foxes have not been observed to contribute significantly to parental care (Strand et al 2000). Therefore, they can not be regarded as true helpers (Moehlman 1989). Moreover, additional adults have been observed at dens during years of both abundant and low food resources (Frafjord 1992), and even in years when the breeding pair has no progeny (Strand et al 2000). Arctic foxes have also been observed to live in permanent groups of up to six individuals on the Mednyi Island (Goltsman et al 2005), and to live in complicated social systems on other islands (e.g., in Iceland, the St Paul Island in Alaska, and Wrangel Island in Russia, Angerbjörn et al 2004). In general, territories and dens are used by only one family group (see a review by Angerbjörn et al 2004). Sometimes, however, territories maintained consist of more than a single breeding pair. In addition to territories, dens may even be shared between several vixens, and more than one litter can be born in a den, i.e., arctic foxes may also breed communally (Frafjord 1992). However, this phenomenon is rare and seems to be restricted to close relatives.

2.1.4 Reproductive failures

Since arctic foxes give birth to cubs in underground dens, it is difficult to assess litter sizes and cub losses. Therefore, the reproductive performance of arctic foxes has been estimated from dead animals and is often calculated based on the number of corpora lutea in ovaries, number of implantation sites (MacEwen and Scott 1957) or number of embryos in uteri (Macpherson 1969). Reproductive performance may also be calculated based on the number of cubs at a den after the emergence of cubs approximately three weeks postpartum (Frafjord 1993a). Thus, estimates of both the litter size and the amount of cub losses in the wild have been based on indirect evidence.

In mammals, litter size is affected by factors such as maternal effects, habitat variance, population density and weather conditions (Stearns and Hoekstra 2000). Habitat variance, population density and weather conditions affect the food supply and thus the amount of energy available for a breeding female. The availability of food has an influence on the development of ovulation, thereby affecting the number of reproducing females. Prenatal cub losses, i.e., offspring loss through resorption of embryos, occur at

various stages of pregnancy (Chirkova et al 1959). On average, even during favourable years, almost one-third of the embryos do not develop to birth. These losses have, of course, a reducing effect on the litter size at birth (Chirkova et al 1959, Tannerfeldt and Angerbjörn 1998). The effect of food stress is strongest in lactating females, resulting in a decrease in cub survival and litter size at weaning (Bronson 1989, Angerbjörn et al 1991).

Cannibalism, i.e., eating members of one's own species (Lawrence 1995), of dead offspring by the mother has been observed in all polytocous mammalian species (Hart 1985). The phenomenon is understandable since eating dead offspring keeps the nest clean in a manner similar to eating placentas and consuming the urine and faeces secreted by the young. Cannibalism may be considered non-adaptive or even pathological behaviour if it involves maternal infanticide, e.g., killing an infant or a normal size or small litter with normal healthy young as a consequence of a behavioural disorder (Hart 1985).

Infanticide is not always a pathological stage, but it can also be considered a natural aspect of the reproductive process (Hrdy 1979, red foxes: MacDonald 1980). Mothers may reduce litter size according to environmental conditions and food supply at the time of whelping by killing some or all of her infants (Day and Galef 1977). Eating one's own progeny may fulfil the nutritional needs, e.g., for proteins, of the mother and thereby increase the survival of part of the litter, or the success of future reproduction (Manocha 1976 in Hart 1985). Moreover, sick infants may be killed and consumed. This occurs also among domesticated carnivores, such as the dog and the cat (Hart 1985).

There are no direct observations of perinatal maternal behaviour in wild arctic foxes, since birth usually occurs in underground dens (Hersteinsson and Macdonald 1982, Hersteinsson and Macdonald 1992). It has been assumed that in arctic foxes, postnatal reduction of litter size by parents is not very likely (Frafjord 1992a). Nonetheless, parents may favour strong cubs with high competitive ability in feeding when food is scarce, thus indirectly leading to the starvation and death of small and weak cubs.

Aggression and fighting associated with food is infrequent among arctic fox cubs (Frafjord 1992a). However, cubs are known to cannibalize their dead siblings when food supplies are insufficient (Garrot and Eberhardt 1983a, Angerbjörn et al 1988), though there is no evidence of siblicide, i.e., the killing of siblings (Arvidson and Angerbjörn 1987, Sklepkovych 1989). Intra-litter aggression is reduced by increasing avoidance between litter mates with age (Frafjord 1992a). Cubs may also abandon their natal den several weeks earlier in areas where prey is low than in those with an abundant supply of small rodents to reduce intra-litter aggression (Fine 1980).

Cub survival is also affected by predation, and diseases. Natural predators for arctic foxes include bald eagles (*Haliaeetus leucocephalus*) and golden eagles (*Aquila chrysaetos*), large hawks (*Buteo*), jaegers (*Genus Stercorarius*), snowy owls (*Nyctea scandiaca*), and mammals such as dogs (*Canis domesticus*), polar bears (*Ursus maritimus*), red foxes (*Vulpes vulpes*), wolves (*Canis lupus*) and wolverines (*Gulo gulo*) (Garrot and Eberhardt 1982, Tannerfeldt and Angerbjörn 1996).

Based on estimates, natural mortality of about two-thirds of the juveniles during their first year is common in Siberia (Bannikov 1970). In years with insufficient food recourses, nearly all the cubs born may be lost during their first year of life (Hiruki and Stirling 1989). In the North West Territories in Canada, the juvenile mortality rates of arctic foxes in 1975-1978, when food availability was low, ranged from 93 to 97 %, whereas the adult mortality was about 40 %.

2.2 Blue fox on farms

2.2.1 General

The first farmed blue foxes, colour variants of the arctic fox, were caught in the wild in Alaska (Einarsson and Skrede 1989) and in the Bering Straits (Broberg and Puustinen 1931) at the end of the 1800s and raised free on small islands. In Europe, blue fox farming experiments started in 1903 in Norway when wild caught Icelandic arctic foxes were farmed together with red and cross foxes on small islands (Norodd Nes et al 1988). In the late 1920s, Norwegians imported some blue foxes from Alaska, and these larger and highly productive Alaskan blue foxes were crossed with a light-coloured and

less productive variant of the wild-caught arctic foxes of Greenland and other North-Atlantic islands (Einarsson and Skrede 1989). Accordingly, the foxes in current farm populations genetically originate from many natural populations and from both those regions with large litter sizes and those with small litter sizes (Frafjord 1993a).

In Finland, a great interest was put in silver fox farming at the beginning of the 20th century, and blue fox farming did not start until the late 1920s (Hernesniemi and Knutar 2000). At the beginning of the production, farmed foxes were housed in groups in ground-floor enclosures and were allowed to breed naturally (Broberg and Puustinen 1931). However, under these conditions, the incidence of aggressive behaviour, endo- and ectoparasites, diseases and cub mortality was high. To reduce these problems, breeding pairs were first offered their own ground-floor enclosures and later raised in wire mesh cages (Broberg and Puustinen 1931).

In the 1960s, the development of an infrastructure for the fur industry, i.e., concentrated feed manufacturing and delivery system, feed quality control, advisor and lobbying organisation, a centralised equipment market and fur sales, enabled an enormous increase in fur production, with production rising from 20 thousand to 1.1 million fox skins during one decade in the 1970s. This great increase in fox production also increased the demand for new breeding animals, which were mainly imported from Norway (Hernesniemi and Knutar 2000).

Increased production was supported by the development of breeding techniques and methods. Artificial insemination of foxes was first introduced in Norway in the 1970s, followed by Finland in the 1980s (Hernesniemi and Knutar 2000). In addition to artificial insemination, breeding efficiency in the selection of breeding animals also underwent great development. In Finland, the most modern method is the Sampo software, which helps the farmer to fill in the ID card, to update animal data and to improve breeding efficiency (FFBA 2008a). Indices in Sampo are calculated by a best linear unbiased prediction (BLUP) method, a well known method also used in livestock breeding (Henderson 1975). In 2007, Sampo was used on 350 fur farms and included 51 percent of the breeding foxes (FFBA 2008a).

In 2007, the production of blue fox skins in Finland averaged 1.9 million skins and accounted for 27 percent of the world's blue fox production (FFBA 2007c). The largest blue fox skin producers in 2007 were China and Finland. Other notable producers included Norway, Poland, Russia and the Baltic countries.

2.2.2 Physical and social housing conditions

In Finland, farmed foxes are most often housed in open-sided outdoor sheds, usually consisting of two rows of cages (Figure 1). The minimum space requirements for farmed foxes are laid down by the European Convention, EC (1999) and the Ministry of Agriculture and Forestry, Finland (Maa ja metsätalousministeriö 16/EEO/1999). The minimum dimensions of a fox cage are 75 x 100 x 70 cm (L x W x H). The minimum space for an adult fox is 0.8 m^2 and 2.0 m^2 for a female with its cubs. The juveniles should be provided with a minimum space of 1.2 m^2 when housed in duets. If more than two cubs are kept together, an extra 0.5 m^2 for each additional cub must be provided. At the moment, these requirements concern all new and replaceable accommodations; in 2010, all accommodations shall apply these requirements. On Finnish farms, the wire mesh cages are usually 115 x 105 x 70 cm (L x W x H), and have a plastic covered wire mesh resting platform (105 x 30 cm, L x W) approximately 25 cm below the cage ceiling. A resting platform if a nest which roof may be used as platform is not available and a gnawing object are required for each cage (Maa ja metsätalousministeriö 16/EEO/1999).

Figure 1. Traditional Finnish two-row sheds for fox housing.

Each breeding vixen is provided with a wooden breeding nest, usually with an anteroom (23 x 47 x 38 cm) and a main room (40 x 47 x 38 cm) approximately two weeks before expected whelping (Hernesniemi and Knutar 2000). The nest is usually placed on the floor of each breeding cage and removed six weeks postpartum. A common belief is that vixens should not be disturbed during the whelping period, i.e., farmers should avoid activity other than feeding (see a review of European Commission 2001). Therefore, opening the nests and inspecting the vixens and cubs is seldom performed until ten days postpartum. The wall between the ante and the main room and the roof of the nest is removed 2-3 weeks postpartum (Finne 1996ab). This may occur earlier in hot weather conditions or if a vixen has a large litter. The nests are often turned side-ways at the time cubs start to get used to solid food at the age of three weeks.

Adult breeding foxes are housed singly (Hernesniemi and Knutar 2000, see also a review of European Commission 2001). During the breeding season, vixens may be moved several times from cage to cage, thus providing a variable social environment. Cubs are housed with their mother until weaning, which occurs at the age of 6-8 weeks. After weaning, cubs are housed in male-female pairs or triplets of two males and a female, or vice versa, until pelting (November-December). These duets and triplets often consist of siblings, but they may also consist of unrelated cubs of different sex. Juveniles are housed singly after breeding selection in November-December. However, if the selection is performed earlier, i.e., at weaning, cubs may be housed in sibling pairs until September-October, or even until December, if both cubs of the pair are selected for breeding.

2.2.3 Management of breeding animals

Traditionally, the breeding animals have been selected for breeding on the basis of their physical phenotype, i.e., the quality of fur, health, litter size and body size of the animals (Peura et al 2004ab, FFBA 2008a). Nowadays, the phenotype of behaviour is also considered according to the degree of foxes' confidence toward humans, which can be tested with a simple behavioural test (Rekilä et al 1997). The test results may be added, for example, into Sampo software and used for the selection of breeding animals. The first selection of breeding animals takes place at the time of weaning (Hernesniemi and Knutar 2000). Unsuccessful vixens are first removed from the

breeding stock. Multiparous vixens are reselected for breeding if they have weaned successfully, for example, over eight cubs and showed good maternal care. Juveniles that have no experience in whelping are often selected for breeding in November-December. All juvenile foxes are generally fed similarly until pelting time, i.e., there is no difference in feeding between females raised for skins or for breeding. As a result, juvenile breeding vixens are often too obese and need to be strictly slimmed down before the breeding season, since reproductive failures are common in fat animals (Sanson and Farstad 2003). Juvenile vixens are selected for breeding mainly according to their phenotypes and indices for fertility, based mostly on the reproductive effort of close relatives (Stranden and Peura 2004). Similar methods are used for the selection of males, though the importance of fertility and fur quality is even more pronounced than in breeding female selection, since each male is used of breeding of several vixens (Hernesniemi and Knutar 2000).

After selection, all females are commonly fed restrictively to allow obese individuals to loose weight and others not to gain weight but remain in good condition (Hernesniemi and Knutar 2000). The feed for fur animals is usually commercially manufactured by feed centres according to recommendations based on scientific research (FFBA 2008b), and planned to fulfil the needs of fur animals during breeding, lactation and growth periods.

Prior to the breeding season, the females are generally transferred into separate sheds in adjacent cages (Harri et al 1999). At the beginning of the breeding season, some males are housed in cages among the vixens. Sometimes, a male is placed in a tunnel next to or on the cages of vixens to induce the development of oestrus. Pheromones and other smells are also believed to induce the development of oestrus; therefore, vixens may be transferred several times from cage to cage before insemination, i.e., vixens without oestrous are transferred to the cages of males or vixens that have already been on heat.

Like wild arctic foxes, farmed blue foxes are also mono-oestrous, seasonal breeders with spontaneous ovulation. Vixens come into heat at the beginning of March, with the heats peaking between mid March and mid April (Farstad 1992). Oestrus is detected visually and often also with an ohmmeter, which measures the resistance of the vaginal mucosa (see Farstad 1992, Boue et al 2000). Most of the blue fox vixens (80 %) are artificially inseminated (FFBA 2008a) generally with good reproductive performance

(Farstad 1998). The amount and colour of the semen are evaluated macroscopically. The mass activity (mass motility of spermatozoa), percentage of live spermatozoa, motility and the frequency of spermatozoa in sperm are evaluated with microscopic examination (Fougner 1992, Jalkanen 1992, Boue et al 2000). After insemination, vixens are relocated to whelp according to their expected whelping order, generally in every second cage (Hernesniemi and Knutar 2000). Thus all vixens get a new cage and new neighbours prior to whelping. This means that the vixens need to establish their new territory and social hierarchy once more (Harri et al 1999).

2.2.4 Reproductive performance and cub losses

Reproductive success may be expressed as reproductive performance per breeding female (RPB) or as reproductive performance per mated female (RPM). Usually, RPB and RPM are evaluated at weaning; on Sampo farms, evaluation occurs approximately 10-14 d postpartum, when cubs are counted for the first time. RPB and RPM are biologically complex variables and affected by many physiological (see summary in Table 1) and environmental factors, and they only illustrate the mean litter size achieved with the number of breeding and mated vixens, respectively. They fail to give additional data about the individual foxes and subcomponents of their reproductive success (Table 1), which have a cumulative effect on RPB and RPM. Thus, details are ignored concerning the problems or weaknesses of the farms. In contrast to RPB, RPM does not take into account the number of vixens without oestrus or vixens that were not inseminated for a particular reason, although these failures can also have a marked influence on RPB and consequently the profitability of fur animal production. On fox farms, reproductive success is generally measured as RPM.

The first problems occurring during the breeding season and affecting RPB are the lack of oestrus or weak oestrus, both of which are more common among primiparous than among multiparous vixens (see Sanson and Farstad 2003, Pylkkö et al 2005). The first factor affecting RPM is the experience of the farmer in detecting the signs of oestrus in females, and skilful inseminations at the appropriate moment (see Jalkanen and Joutsenlahti 1988).

Table 1. Summary (according to Fougner 1991, Ilukha et al 1997, and Valtonen et al 1985) of the subcomponents putatively reducing RPB and RPM through out the breeding season.

Phase of reproduction	Putative problems	Influence
Oestrus	Lack of oestrus Weak oestrus Disturbed oestrus behaviour	High percentage of vixens without oestrus
Ovulation	Low number of released and mature ova Loss of ova before fertilisation	High percentage of barren vixens Low litter size
Fertilization	Low number of fertilized ova Loss of ova before implantation	High percentage of barren vixens Low litter size
Implantation	Loss of embryos	High percentage of barren vixens Low litter size
Pregnancy	Resorption of foetuses Abortion of foetuses	High percentage of barren vixens Low litter size
Whelping	Low number of cubs born High number of stillborn cubs	Low litter size at birth High rate of stillbirths
Nursing - Weaning	Cub losses	High cub losses Low litter size at weaning

Reproductive reduction between inseminations and whelping are seldom observed by the farmer. The loss of ova from release to implantation has been estimated to be 10-30 % (Fougner 1991). Post-implantation deaths until birth account for 15-20 % of the total loss. A Russian study reported that abortion of part of a litter and abnormal birth contributed most to prenatal reproductive failures in blue fox vixens (Ilukha et al 1997). However, abortion seems to occur seldom among blue foxes (0.5 % of barren vixens), thus indicating that resorption of foetuses may be a major factor affecting barrenness (Sanson and Farstad 2003). Reported percentages of barren vixens range from 15 % in Russia (Ilukha et al 1997) to 27 % in Eastern Finland (Smeds 1992). More recent data in Finland (years 1995-2004) show that 35±4 and 14±2 % of mated primiparous and

multiparous vixens, respectively, are unsuccessful reproducers, i.e., barren vixens or vixens that have lost an entire litter (Smeds, unpublished data). As these factors affect litter size at birth, it is not surprising that reported heritabilities for litter size at birth in blue foxes are generally low ranging between 0 and 0.35, with most estimates being at about 0.15-0.20. Accordingly, it seems that litter size at birth is little affected by selection (Valberg Nordrum 1996).

Litter size at weaning is affected by cub losses, which depend on several maternal and environmental factors. A Russian study revealed that of the cubs born, 5.9 % were stillborn and 11.4 % were lost until weaning (Ilukha et al 1997). In blue foxes, only in a very few cases was the whole litter lost. It is more common that some cubs are lost from several litters (Ilukha et al 1997). Reported percentages of females that lose their entire litter have been 1.5 % in Russia (Ilukha et al 1997) and 12 % in Eastern Finland (Smeds 1992).

Generally, the decrease in litter size is greatest during the first week after whelping (Fougner 1991, Ilukha et al 1997, Sanson and Farstad 2003) and in large litters (Ilukha et al 2002). Within the first week postpartum, 80-90 % of the total cub loss has occurred (Fougner 1991, Sanson and Farstad 2003). The main cause for mortality during the neonatal period is the birth of stillborn and weak cubs (Fougner 1991, Sanson and Farstad 2003). In other polytocous species, such as pigs, stillbirths and high occurrence of perinatal deaths (3 days postpartum) have been suggested to be due to competition between the foetuses for space and nutrients in the uterus (Bazer et al 1969). Weakness may also results from too long or hard labour, or maternal effects such as a low amount of milk or inhibited milk secretion (Fougner 1991, Sanson and Farstad 2003). In addition, infections or poisonings through the umbilical cord, respiratory passage or alimentary canal may cause neonatal cub losses (Fougner 1991). Infanticide and cannibalism occur to a minor extent up to three weeks after whelping. Only 0.3 % and 2 % of cub losses have been estimated to result from infanticide (Ilukha et al 1997, Sanson and Farstad 2003, respectively). In other domestic species, killing one's own progeny may sometimes be related to lack of maternal experience, illness of the newborn, hyper-emotionality, or environmental disturbances (Hart 1985).

In blue foxes, dystocia, i.e., problems in whelping, is probably the most common pathologic condition leading to early cub losses after whelping (Sanson and Farstad 2003). Furthermore, dystocia may cause secondary complications, such as retention of foetuses or afterbirth (placenta). Moreover, vixens with these complications may get a severe uterus infection and may not manage to nurse cubs. In Norway, a field study revealed that 25-30 % of the vixens had "changes" in the udder. These changes were thought to be due to infection, circulatory conditions, and blocked teat canals or lactiferous ducts.

According to a statistical model that tested the effects of age of males and females, pregnancy length, number of pups born, year of reproduction, feed kitchen and farmer on cub losses during first three weeks postpartum, the most important factors affecting cub losses in blue foxes were the age of the vixen, the farmer, and the number of cubs born (Sanson and Farstad 2003). The farmer may also have an influence on the level of prenatal stress experienced by the pregnant vixen. It has been shown that prenatal stress affects the development and survival of offspring in blue foxes (Braastad et al 1998). If vixens feel secure, they behave calmly and stay with cubs when the cubs are at the most vulnerable age probably reflecting as lower cub losses (Silver foxes: Braastad 1994, Braastad 1996). The strong effect of the farmer may indicate that management is the most important explanation for the variation seen in perinatal cub losses (Sanson and Farstad 2003).

It is generally believed among farmers that reproductive failures in foxes are caused by environmental disturbances during whelping and the nursing period. Acute stressors, such as thunder, rainstorm, smoke or the noise of aircraft, are believed to evoke panic reactions in new mothers, leading to infanticide or the rejection of offspring. Moreover, wild animals on farms are also believed to irritate farmed foxes. Other physical factors, such as high temperatures, are believed to stress foxes and to further increase existing problems.

In general, primiparous vixens have lower reproductive performance than multiparous vixens (Fougner 1991, Smeds 1992, Hernesniemi and Knutar 2000, Sanson and Farstad 2003). This difference can be explained by two factors. Firstly, multiparous vixens have already undergone selection for good reproduction properties. Secondly, multiparous

vixens are kept in good shape through the year, i.e., they are not overfed in the autumn like the young unselected vixens. Therefore, the multiparous vixens do not generally suffer from reproductive failures resulting from overweight (Sanson and Farstad 2003). Overweight at the beginning of the breeding season has been shown to cause weak oestrus, lack of oestrus, difficulties in insemination, barrenness, birth complications and birth of cubs with reduced chances of survival (Sanson and Farstad 2003). Recently, it has also been suggested that young vixens may not reach maturity during their first breeding season (Pylkkö et al 2005).

In Finland, there has been a tendency towards decreased litter sizes (Peura and Stranden 2003) and RPM over the last decades in contrast to e.g., Norway where RPM has tended to increase (Figure 2). In 2007, RPM for farmed blue fox vixens in Finland was less than five cubs for the first time (FFBA 2007b). In Russia, the reported RPM has been better than in Finland, 7.8 cubs (Ilukha et al 1997).
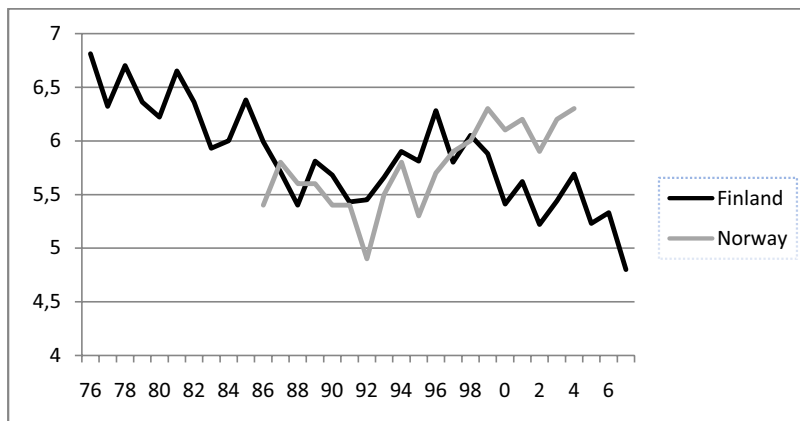
Figure 2. The development of RPM in blue foxes in Finland and Norway during the last decades.

2.2.5 Welfare and reproduction

Decreased reproductive performance in blue foxes may be due to several reasons. Impaired reproduction may be a consequence of selecting for larger size (Peura and Stranden 2003) or the inferior quality of sperm due to genetic failure in males (Pylkkö

et al 2005). It can also reflect the negative effects of unsatisfactory management (farmed foxes: Sanson and Farstad 2003) or inappropriate housing conditions (Broom and Johnson 1993, farmed foxes: see, e.g., Bakken et al 1994, Nimon and Broom 2001). It has also been claimed that the barren environment provided for farmed foxes has led to poor reproduction and abnormal behaviour, such as maternal infanticide (Nimon and Broom 2001). Therefore, several research projects have been carried out to evaluate the welfare of farmed foxes and to develop alternative housing solutions in an effort to increase reproductive success (see a review of European Commission 2001).

The welfare of animals in intensive husbandry systems was first defined in 1965 in terms of five freedoms (Brambell Committee 1965). These original definitions were redefined later by the Farm Animal Welfare Council, FAWC (1993).

The five freedoms are

"1) Freedom from thirst, hunger and malnutrition — by ready access to fresh water and a diet to maintain full health and vigour.

2) Freedom from discomfort — by providing an appropriate environment including shelter and a comfortable resting area.

3) Freedom from pain, injury and disease — by prevention or rapid diagnosis and treatment.

4) Freedom to express normal behaviour — by providing sufficient space, proper facilities and company of the animals own kind.

5) Freedom from fear and distress — by ensuring conditions that avoid mental suffering".

These five freedoms include the three approaches for scientifically defining animal welfare. These approaches stress differently feelings, functioning and natural living (Duncan and Fraser 1997, Fraser et al 1997) but are still closely related to each other and partly overlap (Fraser et al 1997, Lund 2002).

Several welfare indicators can be used to analyse welfare status in animals (Broom and Johnson 1993, for farmed foxes see a review of European Commission 2001); however,

despite the numerous methods developed to measure welfare, assessing welfare in a scientific manner is not simple (e.g., Rushen 1991, Duncan and Fraser 1997). One parameter should not be used as a status of stress or welfare alone but in conjunction with other parameters (e.g., Rushen 1991, Broom and Johnson 1993). However, it has been suggested that welfare research has tended to rely too heavily on inadequately validated physiological, immune and behavioural measures of welfare, and that more weight should be given to health problems, which may be major threats to animal welfare (Rushen 2003). Furthermore, too little attention has been placed on the quality of stockmanship, nutritional effects and the effects of breeding on the welfare of animals.

Reduced reproductive efficiency may be the result of stressors associated with animal housing, human-animal relations and management (Moberg 1991). Stress, defined as a biological response elicited when an animal perceives a threat to its homeostasis, may induce changes in the secretion of pituitary hormones (Moberg 2000). This may lead to altered metabolism, immune competence and behaviour, as well as failures in reproduction causing decreased production, reduced reproduction or increased mortality and morbidity. Thus, reproductive performance may be considered and used as an indicator of welfare. Although the pathophysiological mechanisms describing stressors disrupting reproduction are not fully understood, the stress-induced secretion of adrenal glucocorticoids seems to be of special importance (Borrel et al 2007). These steroids can have an effect on both the synthesis and secretion of gonadotropins. In addition, corticoliberin (CRH) and adrenocorticotropin (ACTH) may affect the regulation of the hypothalamic-pituitary-gonadal axis. Therefore, folliculogenesis and ovulation are the most vulnerable phases of reproduction to stress, though implantation of embryos and the expression of sexual behaviour may also be at risk. Stress responses to short-term (acute) stressors may differ from those to long-term stressors: acute stressors often fail to affect reproduction. However, acute stressors may prevent animals from achieving normal reproductive success if the stressful stimuli occur during the most vulnerable periods of reproduction, i.e., during the folliculogenesis and ovulation (Moberg 1991).

It has been argued that the main welfare problems currently affecting fox farming are foxes' fear of humans and failures in reproduction, e.g., lack of oestrus, week oestrus, barrenness, neglecting cubs and infanticide (see a review of European Commission

2001), which may be closely related to each other. However, several studies have examined the welfare of farmed silver and blue foxes during breeding season. These scientific attempts to improve foxes' welfare have focused on the housing environment, e.g., space per animal, resting platforms, enrichment objects, and semi-natural environments (e.g., Jeppesen and Pedersen 1990, Harri et al 1995, 1997, Korhonen and Niemelä 1995, 1996ab, 2000, Malm 1995, Ahola et al 1996), nest configuration and location (e.g., Moss and Östberg 1985, Haapanen et al 1992, Pedersen and Jeppesen 1993, Braastad 1994, 1996, Harri et al 1998ab, Rekilä et al 1998, Mononen et al 1999, Pyykönen et al 2002a, Korhonen et al 2006), social organization of breeding vixens before and after the breeding season (e.g., Kullberg and Angerbjörn 1992, Korhonen and Niemelä 1993, Bakken 1994, Korhonen and Alasuutari 1995, Korhonen et al 1997, Pyykönen et al 1997, 2002b, 2004, Strand et al 2000), and selection of more confident breeding animals (e.g., Nikula 1997, Kenttämies and Smeds 2000, Nikula et al 2000, Nordrum et al 2000).

Both farmed fox species, *V. vulpes* and *V. lagopus*, can be regarded as highly ranging animals. It is suggested that widely ranging territorial animals in captive environments should be provided with more space, multiple den sites, greater daily environmental variability or novelty and more control over exposure to aversive or rewarding stimuli (Clubb and Mason 2007). In farmed foxes however, attempts to improve reproductive performance with single environmental factor have in general failed to give a statistically significant relationship between housing design and reproductive success (Harri et al 1998a). Yet, in silver foxes, tunnel nests (Braastad 1994, 1996) and top nests (Pyykönen et al 2002a) have been proposed as having a positive effect on RPM and behaviour in primiparous breeding vixens (Braastad 1996). In addition, blue fox vixens in a breeding nest with an entrance tunnel have been reported to wean more cubs per breeding female than blue foxes in traditional breeding nests (Moss and Östberg 1985). Similar results have been reported by Haapanen et al (1990), who concluded that nest type affects RPM, but only after other more important factors have been taken into account. Mononen et al (1999) found no difference in RPM or cub losses between vixens housed with a top nest (situated on the roof of the cage) and vixens housed with a traditional floor nest. However, in primiparous vixens, there were more barren vixens in floor nests than in top nests.

Social environment is known to affect the reproductive success in silver foxes (Bakken 1994, Harri et al 1995, Pyykönen et al 1997, 2002b). Dominant vixens or vixens with higher competition capacity have better reproductive success than those subdominant vixens even when housed in separate cages. Moreover, low status vixens are more likely to commit infanticide, albeit previously infanticidal vixens may wean more unharmed cubs in the following breeding season if they are visually and spatially isolated from other vixens on the farm (Bakken 1994). No comparable studies on the effects of social factors on reproduction in blue foxes exist in traditional farming conditions. However, several studies have been carried out to describe reproductive success in blue foxes when housed in social groups in semi-natural environments (Kullberg and Angerbjörn 1992, Korhonen and Alasuutari 1994, Strand et al 2000). When housed in groups, only the dominant pair reproduces. In addition, the parent foxes provide more care to the young than the additional group members. In semi-natural environments, the dominant vixen with a male may succeed in reproduction as well as vixens in traditional farming conditions but other vixens in these semi-natural conditions usually fail in reproduction (Malm 1992). Because the results are too heterogeneous, any definite conclusion concerning the social environment and the reproductive success in blue foxes could not have been drawn (Harri et al 1998a).

Selection for more confident foxes may slightly increase reproductive success of vixens on a population level, and more clearly other production parameters, such as body size and fur quality (Nikula 1997, Kenttämies and Smeds 2000, Nikula et al 2000). Selection of "docile" or "tame" individuals for breeding enhances the progress of domestication (Grandin and Deesing 1998, Price 1999) and is possible in both farmed fox species (the silver fox: Belyaev et al 1985, Trut 1999; the blue fox: Nikula et al 2000, Nordrum et al 2000). In addition, pre- and post-weaning handling has been shown to have positive consequences for later behaviour of growing blue foxes and seems to adapt the foxes better to farming routines including human proximity and human-animal interactions (Pedersen and Jeppesen 1990, Pedersen 1991, 1992, 1993ab, Harri et al 1998b, Pedersen et al 2002). With the help of early handling a positive human-animal relationship (HAR) has been established also in other husbandry animals, e.g., cattle (Boivin et al 1994), pigs (Hemsworth et al 1986), sheep (Mateo et al 1991), horses (Jezierski et al 1999), and dogs (Wright 1983). Apart from post-weaning handling, prenatal stress, i.e., the stress experienced by the pregnant mother, have been shown to

have an effect on the behaviour of the developing fox cubs and survival of offspring in blue foxes (Braastad et al 1998). In addition, prenatal stress results in a significant reduction in hormone secretion and the morphometry of the reproductive organs of offspring (Osadchuk et al 2001, 2003ab). Thus, the farmer has an important role on the level of the behavioural stress experienced by animals in intensive housing systems (Braastad et al 1998, Moberg 2000, Pedersen et al 2002).

3. OBJECTIVES

For profitable animal production, it is important that most of the breeding vixens succeed in reproducing and have large litters with good cub survival. These factors can also be used as a measure of welfare, since (unpleasant) stress may have a negative effect on reproductive performance, i.e., stress may reduce fitness. With regard to fur animal production, it has been claimed that traditional housing systems reduce the welfare of farmed foxes. Reduced welfare may be reflected in the increased incidence of abnormal behaviour, including maternal infanticide, and impaired reproduction success.

The aim of this thesis was to describe maternal behaviour and the incidence of maternal infanticide during the whelping period, as well as to evaluate how common such a phenomenon is among blue foxes (I). In addition, the effect of acute environmental stressors, i.e., aviation noise, (V, V[u]) and handling (V[u]), on the incidence of infanticidal behaviour, cub losses and reproductive performance in general (V) and in behaviour and physiology (V[u]) were of interest. Alternative housing solutions that might have positive effects on reproductive performance and welfare in blue fox vixens were also under evaluation (II-IV). The alternative housing and breeding systems studied were designed to resemble more closely the natural features of the arctic foxes' breeding habitat than the present housing conditions do. Compared to the traditional breeding practice, the alternative housing (II, III, IV) and breeding (III) systems introduced in this thesis included changes either in the foxes' social environment (II), physical environment (IV) or both (III). The main hypothesis underlying the experimental design was that if the traditional breeding conditions have adverse effects on foxes' welfare, then positive changes in their housing environment should enhance their RPM.

4. MATERIAL AND METHODS

The material and methods used in the original papers (I-V) of this thesis are summarised below. A more detailed description of the material and methods can be found in the original papers republished with the thesis. A summary of the breeding experiments is presented in Table 2. This thesis also contains previously unpublished data. The unpublished data is based on the studies presented in the original papers (III, V) and marked with superscript (III [u], V[u]). The studies were approved by the Institutional Animal Care and Use Committee of the University of Kuopio, Finland (I-IV) or the State Provincial Office of Eastern Finland (V).

4.1 Animals and housing

The experiments were performed during the breeding seasons over the years 1996-2004 at the Research Station of the University of Kuopio (Juankoski, Finland) with 395 females and 12 males in total. In addition, a private farm was also used as an experimental farm in V. All the animals in I-IV originated from the Research Station. In V, both multiparous vixens and a majority of the primiparous vixens originated from the private farm, though some of the primiparous vixens originated from the Research Station.

In addition to the breeding vixens, ten non-breeding one-year-old vixens were also used for physiological analyses of stress during noise exposures, handling and transportation in V[u]. These non-breeding vixens originated from the Research Station and were transported with a car trailer to the private farm where they were exposed to aviation noise. For breeding experiments, only primiparous blue fox vixens were used in III, in contrast to the other experiments (I, II, IV, V) in which both primiparous and multiparous vixens were used (Table 2). All vixens were born in standard fox cages (115 x 105 x 70 cm, L x W x H) in wooden two-room (i.e., an anteroom and a main room) floor nests. Experimental vixens were selected for breeding in either October and fed restrictively thereafter (V, V[u]) or November-December and fed restrictively approximately three months before the start of the breeding season (I-V). Experimental vixens were selected for the experimental groups either before the actual breeding season (II, III), or after insemination, i.e., when only vixens showing oestrus were used

(I, IV, V). The males used in the experiments and for AI were breeding males originating from the Research Station (I-IV) or the private farm (V).

During each breeding season, vixens were housed in standard fox cages (I-V). Each cage was equipped with a resting platform (105 x 25 cm) and a feeding plate. In III, some vixens were also housed in so-called row cages made by connecting two (double-cage system) or three standard fox cages (triple-cage system), or in ground floor enclosures (see Figure 3). Two of these enclosures measured 5 x 10 m (L x W) and four 7.5 x 15 m. Each enclosure was furnished with a resting shed. The resting sheds consisted of a slightly tilted iron-sheet roof (170 x 250 cm, L x W) that was 115-165 cm above the ground level, a wooden floor (105 x 175 cm, L x W) 40 cm above the ground level, and a plastic covered wire mesh resting shelf (210 x 30 cm, L x W) 80 cm above the ground level. The space per individual fox was 16.7 or 37.5 m^2 in enclosures, and 1.2 m^2 in cages.

Figure 3. One of the outdoor enclosures with two female siblings and a male. Photo: Tarja Koistinen.

Table 2. A summary of the experiments and groups. A total of 395 females and 12 males were included in the thesis. PP=primiparous vixens, MP=multiparous vixens, AI=artificial insemination, NB=natural breeding, C=control group, E=experimental group, SSE=stable social environment, SC=single-housing in a cage, PC=sister pairs in a cage environment, PE=sister pairs in an enclosure, RPM=cubs per mated vixen.

Paper	Season(s)	Vixens PP MP	Topics	Groups
I	1996-1998	10 6	Maternal behaviour and incidence of infanticide	Whelped vixens
II	2001-2002	83 31	Social environment and housing density	C: Unstable social environment with high animal density (HD, i.e., housing in adjacent cages) E: SSE with low hosing density (LD, i.e., housing in every fourth cage)
III	2003	48 0	Social environment and breeding system, i.e., NB vs. AI	AI-SC: AI, single-housing in cage environment, SSE AI-PC: AI, sister pairs in cage environment, SSE NB-PC: NB, sister pairs with a male in cage environment, SSE NB-PE: NB, sister pairs with a male in an enclosure, SSE
III[u]			The effect of breeding weight on oestrus, barrenness and weaning success	Vixens without oestrus, barren vixens, and vixens that succeeded in weaning their cubs
IV	2000	25 33	Nest location and number of available nests	C: Top nest E: Two nests, a top nest and a floor nest
V, V[u]	2004	90 69	Acute environmental stressors: aviation noise (V), and handling and transporting (V[u]) The effect of timing of selection and feeding level on RPM (V[u])	C: No exposure to acute stressors (V), early selected and restrictively fed PP vixens (V[u]) E: 3-5 aviation noise exposures (V), early selected and restrictively fed PP vixens (V[u]) E[u]: Two aviation noise exposures, handling and transportation

Breeding vixens were provided with a nest approximately two weeks before the expected whelping date, i.e., in April-May (I, II, IV, V) or already in January (III). Generally, vixens were artificially inseminated (I-V), although unsupervised natural breeding (NB) was also used (III, see Table 2). The development of oestrus was determined visually, and around oestrus, the electrical resistance of the vaginal mucosa (see Møller et al. 1984) was measured daily in studies I-V, except for the two NB groups in III.

All experimental foxes were fed according to the Finnish recommendations (FFBA 2007d) with commercial feed manufactured by a feed centre (Ylä-Karjalan Rehu Oy, Valtimo). Water was available ad libitum.

4.2 Treatments and measurements

4.2.1 Maternal behaviour and incidence of infanticide

The incidence of abnormal behaviour, such as maternal infanticide, may result from inappropriate housing conditions and indicate reduced welfare (Nimon and Broom 2001). The behaviour of blue fox vixens was analyzed to describe and quantify periparturient maternal behaviour with special emphasis on possible infanticidal behaviour or maladjustment to traditional housing conditions using a traditional or tunnel nest (I). The periparturient behaviour of the vixens in the nests was video recorded during two weeks and analyzed for six different periods. These periods were five days pre-partum (-5d) and one day (-1d) pre-partum, parturition, and one (+1d), two (+2d) and three (+3d) days postpartum. The percentages of observations spent in different behavioural patterns were calculated for 24-hour periods except for the parturition period, which was defined as the time period extending from the birth of the first cub to the birth of the last cub, the length of which varied individually.

Instantaneous sampling (IS) at a 1-min interval was used for quantitative analysis of the behavioural states (Martin and Bateson 1993). Behavioural sampling (Martin and Bateson 1993) was used to obtain a more detailed description of periparturient behaviour throughout the video recording(s) (I). Behavioural sampling made it possible to observe behavioural patterns that were important but of short duration and seldom

occurring. Therefore, the data from behavioural sampling were not quantified but only presented descriptively. Additionally, the cubs were counted and the subcomponents of reproductive success (see Table 3 for the variables) were calculated based on the data from cub counting.

4.2.2 Reproduction and cub losses

It was assumed that the better the reproductive success, and the lower the percentage of unsuccessful vixens, and the lower the cub losses, the better the housing system and the welfare of the vixens and their cubs (Moberg 2000). Thus, RPM with its subcomponents was the main variable assessed in all papers and was calculated separately for primiparous and multiparous vixens based on the data from cub counting (I-V) (Table 3).

Table 3. Parameters calculated and used for comparisons of reproductive success between the experimental groups.

Variable	Definition	Paper
RPB	Number of weaned cubs per breeding vixen	II-V
RPM	Number of weaned cubs per mated vixen	I – V, V[u]
Succeeded	Percentage of breeding vixens that weaned cubs	I - V
No oestrus	Percentage of vixens without any signs of oestrus	II, III, III[u], V
Barren	Percentage of inseminated vixens that did not whelp	II - V
Lost all	Percentage of inseminated vixens that whelped but lost their entire litter	II - V
Weaned	Percentage of inseminated vixens that whelped and weaned at least one cub	I-V
Litter size	Number of cubs per whelping vixen	I-V
Stillborn	Number of stillborn cubs per whelping vixen	I, II, V
Cub losses	Percentage of dead cubs for the vixens that whelped	I -V

In order to accustom the vixens to human presence, the nests were inspected daily over a period extending from two weeks prior to the expected whelping until the cubs were born (II-V). The number of cubs was counted either from video recordings (I) or

directly from the nests from birth to weaning (II-V). Dead cubs that were found were removed from the nests for inspection (II-V). The classification whether a cub was stillborn or had lived after birth was done either on the day of birth or one day postpartum by a lung flotation test (Nara and First 1981) (II, IV, V) or by monitoring stillbirths from the video recordings (I). In the video recordings, a cub was defined dead when it had become separated from the huddling group and remained immobile during the vixen's next visit outside the nest (I). Bite wounds were also analysed from dead cubs in V. When vixens had two nests in use, the location of the cubs was recorded at the same time as inspection of the nests and the cub counting (IV).

4.2.3 Social environment

Social environment is known to regulate reproduction in small canids (Geffen et al 1996). Moreover, in many species, dominant vixens suppress the reproduction of subordinates. On fur farms, such regulation may also occur as foxes are housed in high densities and their social environment is disturbed due to relocations of animals. In the present thesis, breeding vixens were housed either singly (I-V, V^u), in sister pairs (III), or sister pairs with a male (III). In III, the foxes were assumed to have a stable social environment, though the social hierarchy of foxes in groups could change. Vixens were either provided with a permanent breeding cage or enclosure in August (III) or from January (II, III) onwards, or transferred to their breeding cages after insemination in March (I, II, IV, V). In other words, social environment was stable from August (III), January (II, III) or from March (I, II, IV, V) onwards.

The social conditions of foxes were also manipulated using different housing densities. After insemination, vixens were housed either in adjacent cages (II), every second cage (I, III, IV, V) or in every fourth cage (II) either in the two rows of sheds (I-V) or in enclosures (III). The row cage systems were separated from each other with two empty cages (III). In the enclosures, foxes had visual contact with each other, as well as contact between one enclosure and another (III). Two enclosures were always connected to each other with a separating wire netting forming a unit. The distance between each of the three enclosure units was approximately 2-3 m. In pairs, foxes were assumed to have stable social environment (III), though the social hierarchy of foxes in groups could change. The effect of social environment on the reproductive success was

assessed by comparing the subcomponents of reproductive success between vixens that were housed in different social environments (see Table 3 for the variables).

4.2.4 Nests

In the wild, arctic foxes prefer to use the same dens season after season, and use of multiple dens is characteristic of this species. In addition, artic fox dens are often complex structures with several entrance tunnels located higher than its surroundings (Anthony 1996). In the present thesis, it was assumed that complicated nests resembling the nests of arctic foxes could also be used on farms to enhance the welfare of foxes.

The studied nest types are shown in Figures 4a-c. Vixens were provided with either a standard fox nest (I, II, IV, V), top nest (IV) or a tunnel nest, i.e., a nest with a tunnel entrance (I, III). All nests had an anteroom and a main room. In standard fox nests, the anteroom and the main room measured 30 x 43 x 37 cm and 45 x 43 x 37 cm (L x W x H), respectively. In top nests, corresponding measures were 32 x 44 x 33 cm and 44 x 44 x 33 cm. Top nests had an entrance (diameter 20 cm) to the anteroom of the top nest situated on the cage's ceiling over the resting platform. Between the two rooms of the top nests there was a round opening (diameter 20 cm). The front wall of the top nests could be opened. Access to the top nests was made easier by mounting a wire mesh "ladder" (30 x 105 cm) in all cages. The ladders leaned to the platforms at a 50 degree angle. Tunnel nests with a tunnel entrance of 45 x 20 x 22 cm were either standard nests or nests with an anteroom measuring 23 x 47 x 38 cm (L x W x H), and a main room 40 x 47 x 38 cm (III). Standard fox nests were placed on the floor of each breeding cage (I, II, IV, V), top nests on the roof of each cage (IV) and tunnel nests into each vixen's neighbouring cage (I, III) or at both ends of each row cage system (III). The foxes had no access to the nest cages but could use only the interior of the nest. In IV, some vixens received both a standard floor nest and a top nest.

The effect of the nests on reproductive success was analysed by comparing the subcomponents of the reproductive success (see Table 3 for the variables) between the vixens housed in different types of nests. In the experiment where some of the vixens had two nests in use, the location of the cubs was recorded concurrently with inspection of the nests and the cub counting (IV).

Figure 4a. A standard floor nest.

Figure 4b. Top nests on the roofs of standard fox cages.

Figure 4c. A tunnel nest used by a silver fox.

4.2.5 Acute stressors: aviation noise and handling

Acute stress is known to negatively affect reproduction (Moberg 2000). In the present thesis, experimental vixens were exposed 3-5 times to severe aviation noise for duration of 14-65 minutes, with maximal noise inside the sheds ranging from 111.8 to 121 dBA during pregnancy and the nursing period (V, V^u). Aviation noise originated from an F-18 Hornet interceptor and a Hawk Mk 51 jet trainer.

Variables related to reproductive success (see Table 3) of blue fox vixens on the aviation noise farm were analysed and compared with those of vixens on the farm without aviation noise (V). The behaviour of the vixens (N=22) was video recorded on three consecutive days at the 4th and 5th noise exposures: the day before (EXPO-1d), the day of (EXPOd), and the day after (EXPO+1d) the 4th and 5th noise exposures (V^u, Figure 5). All video recorded vixens at the 4th and 5th exposures had cubs aged 0-14 days. Accordingly, the vixens that were video recorded were different vixens during these exposures. Instantaneous sampling at 10-min intervals was used for quantitative analysis of the behavioural states (Martin and Bateson 1993). The behavioural categories for 24-hour observations were *active*, *resting*, *sitting* and showing *stereotypic behaviour*. In addition, the use of space inside the cage was divided into four categories:

in the nest, on the nest, on the cage floor and on the resting platform. The percentage of observations spent in different behaviours was first calculated for 24-hour periods (EXPO-1d, EXPOd and EXPO+1d). The use of nests was also analysed for the 60-min period before (EXPO-1h), during (70 min, EXPO), and 60 min after (EXPO+1h) the 4th and 5th noise exposures for the days EXPO-1d, EXPOd and EXPO+1d.

In addition to behavioural responses, the physiological response to acute stress was also assessed. The stress-induced hyperthermia (SIH) test is based on the notion that the presence of humans causes an acute reaction in an animal shown as changes in the animal's rectal temperatures (Moe 1996, Bakken et al 1999). In the present thesis, it was hypothesized that if human presence causes SIH and increases body temperature (T_b) values, other acute stressors, such as aviation noise, would also lead to raised T_b values (V^u), thus allowing responses to different stressful stimuli to be compared.

Figure 5. The video recording equipment in V^u. Photo by Jyrki Juntunen.

T_b was measured as deep body temperature from the ten non-breeding blue fox vixens equipped with thermo-sensitive loggers (iButton Thermochron, model DS1921H, resolution 0.125 °C, Dallas Instruments, USA) coated with paraffin and inserted into their abdominal cavity (by Dr. Petteri Nieminen and Dr. Anne-Mari Mustonen from the University of Joensuu). The loggers registered the deep body temperature every minute,

giving altogether 820 individual data points for each experimental animal for the analyses (V^u). The transportation of these foxes to the aviation noise farm occurred approximately a week before the 4th noise exposure, i.e., in late May, a week before their first exposure to aviation noise and the measurements of body temperatures (T_b). The non-breeding vixens were located into the front part of the shed, where the primiparous vixens that were expected to whelp last were housed. These non-breeding vixens were exposed to aviation noise during the 4th and 5th noise exposures. In addition to aviation noise, these vixens were also exposed to handling on the day after the 5th noise exposure (V^u). This handling included human contact, transportation, and changes in the foxes' social environment. The foxes were first caught from the cage with neck tongs and removed to transporting cages in a random order. The transporting cages were loaded in a car trailer. The foxes were then transported a distance of 14 km and randomly moved to cages at the Research Station. This handling period (HANDLING) lasted approximately 130 minutes, i.e., it was twice as long as the noise exposure periods, but occurred approximately at the same time of the day as the two last noise exposures (V^u).

T_b was measured during three exposures, i.e., during the 4th and 5th noise exposures (EXPO4 and EXPO5) and during HANDLING, and on a day without exposure, i.e., on the day after the 4th noise exposure (BASE, V^u). The T_b data was analysed for three periods during these four treatment days. These three periods consisted of a 60 min period before (-1h) and after (+1h) the exposures, and the period of exposures, i.e., 70 min period of aviation noise (EXPO4 and EXPO5) or 130 minutes period of handling (HANDLING) or 60 min period without exposure (BASE) (V^u).

4.2.6 Body mass

Overweight at the beginning of the breeding season is believed to be a major cause for most of the reproductive failures in blue foxes (Hernesniemi and Gnutar 2000, Sanson and Farstad 2003). Therefore, the weight of primiparous vixens was assessed in III^u. The vixens were weighed in September (BM_1), December (BM_2) and at the beginning of the breeding season at the beginning of March (BM_3) (III^u). The relative change of body mass ($[\Delta BM_{rel} = (BM_2 - BM_3) / BM_2] \times 100 \%$) from December to the beginning of March was calculated for the vixens (III^u). The effect of BM_3 and ΔBM_{rel} on weaning

success (weaned cubs vs. no weaned cubs) was analysed for all vixens, and the effect of BM_3 and ΔBM_{rel} on the number of vixens having oestrus, barren vixens, and successful vixens was analysed for the vixens in the AI groups (III[u]).

4.3 Statistical analyses

Statistical analyses were performed using SPSS statistical software. A more detailed description of the statistical methods used can be found from the original articles (I-V) attached to this thesis. For the unpublished data, the Friedman two-way analysis of variance by ranks was used to compare differences in behavioural patterns during the 24-hour periods between days EXPO-1d, EXPOd and EXPO+1d (V[u]). Differences in the use of nests between the periods (EXPO-1h, EXPO, EXPO+1h), the days (EXPO-1d, EXPOd and EXPO+1d) and noise exposures (4th and 5th) were analysed with the General Linear Model (GLM) for repeated measures (between-subjects factor: noise exposures, within-subject factors: day and period) (V[u]). Differences between the days (4th noise exposure, base level, 5th noise exposure and handling) and periods (EXPO-1h, EXPO, EXPO+1h) in T_b were analysed with GLM for repeated measures (within subjects factors: day, period). A simple contrast was used to test differences among the days (4th noise exposure, base level, 5th noise exposure and handling) (V[u]).

The difference in RPM between early and late selected primiparous vixens was compared with the T-test (V[u]). Differences in the BM of vixens between different time points were analysed with GLM for repeated measures (III[u]). The Linear Mixed Model was used to assess the effect of BM_3 and ΔBM_{rel} on weaning success (weaned cubs vs. no weaned cubs) for all vixens (III[u]), and on the number of vixens having oestrus, barren vixens, and successful vixens in the AI groups.

5. RESULTS

5.1 Maternal behaviour and incidence of infanticide

Proper maternal behaviour was exhibited by both the primiparous and the multiparous vixens before, during and after whelping (I). There were no major differences in the behaviour between primiparous and multiparous vixens. Primiparous vixens were probably more restless than multiparous vixens before and after whelping, as shown by shorter amount of time spent inside the nest.

During parturition, the vixens licked their genital area and actively participated in their deliveries (I). Between the deliveries of individual cubs and after parturition, the vixens showed cub care and nursing behaviour. Most importantly, no obvious signs of maternal infanticide were observed. However, small and weak cubs were observed, and these cubs succumbed soon after birth. The vixens were occasionally found to move these weak, or probably dead, cubs into the middle of the huddling group. In some cases, the vixens concealed the dead cubs in corners of the nest under fur tangles before eating these cubs, which took place some minutes, hours or days later. The time spent in cub care decreased during the three postpartum days. Generally, individual cubs received less attention and care from its mother in larger than in smaller litters.

Despite the proper maternal care exhibited by the vixens, cub losses from birth to weaning were 33 % and 17 % in the primiparous and in the multiparous vixens, respectively (I). Over 65 % of all cub losses occurred during the first three days postpartum and over 80 % during the first week. In the multiparous vixens, all cub losses occurred during the first three days postpartum, whereas the primiparous vixens also tended to loose some cubs later (I).

5.2 Social environment

Social environment had little effect on RPB or RPM (II, III). In the multiparous vixens, RPM tended to be higher in the vixens housed in permanent breeding cages combined with lower density than those in an unstable social environment with high density (II). In the groups with a male, only one vixen out of 24 vixens whelped. However, her cubs

were destroyed within two weeks postpartum (III). As a result, it was not possible to assess the effect of males in a group on weaning success. In AI vixens, RPM was lower in pair-housed than in single-housed vixens (III). Only in one pair was a communal breeding system displayed and the cubs weaned by the vixens. Single-housed primiparous blue fox vixens reached high RPM (5.9±4.6 weaned cubs per mated vixen) when housed in stable social environment in every second cage with a tunnel nest (III). The RPM in these primiparous vixens was as good as the national average (5.6 cubs) (Smeds, unpublished data) for the same year in blue foxes (including both primiparous and multiparous vixens) on private farms that use the Sampo software.

5.3 Nests

Although not studied *per se*, singly-housed primiparous vixens with a tunnel nest reached high RPM (5.9±4.6 cubs). When a top nest or two nests (floor and top nest) were available, no difference in RPM was observed between primiparous and multiparous vixens (IV). Multiparous vixens had low RPM (5.6 cubs), while primiparous vixens succeeded equally well in housing systems with one nest (top nest) or two nests (top and floor nest). The additional nest had no clear effect on RPM in blue foxes (IV). In multiparous vixens, cub losses were higher in vixens that had only a top nest in use than in those having two available nests (top and floor nest). When two nests were available, the majority (86 %) of the primiparous vixens whelped in the floor nest, whereas the majority (73 %) of the multiparous vixens favoured the top nest for whelping. Approximately 43 % of the vixens with two nests were observed to have cubs in both of the available nests at least once.

5.4 Acute stressors: aviation noise and handling

In blue fox vixens, acute exposures to aviation noise had no effect on RPM, incidence of infanticide or cub losses (V). Nevertheless, a response in behaviour and physiological parameters could be observed (V[u]). There were no differences in the time spent in different behavioural patterns during the 24-hour observation periods EXPO-1d, EXPOd, and EXPO+1d when the data from 4th and 5th exposures were pooled (Figure 6).
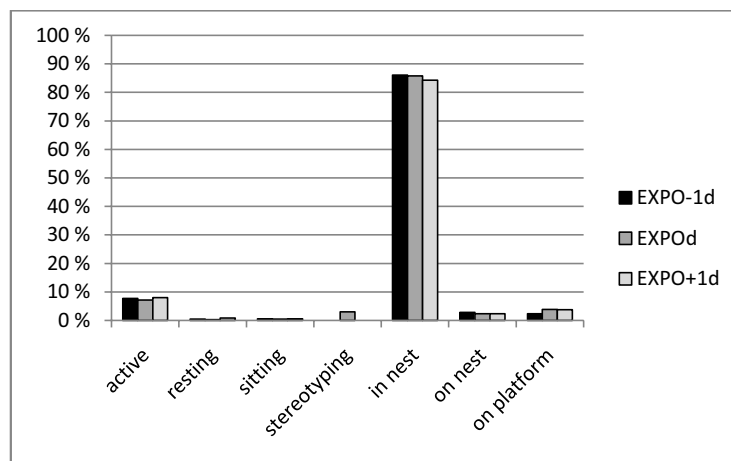
Figure 6. The percentage of time spent in different behavioural patterns and location of foxes in their home cages during the 24-hour observation periods on the day before (EXPO-1d), on the day of (EXPOd), and on the day after (EXPO+1d) the aviation noise exposures. Data from 4th and 5th exposures pooled. P>0.05 (Friedman two-way analysis of variance by ranks) for all behaviour categories (N=22). Statistical difference between the days P>0.05.

The results showed, however, that the vixens exposed to aviation noise during the 5th noise exposure spent less time inside the nest during the exposure (EXPO) and during the same time period on the day after the 5th noise exposure (EXPO+1d) than during the other periods (EXPO-1h, EXPO, EXPO+1h) on other days and on the day of the 4th noise exposure (interaction exposure*day*period, P = 0.037, Figure 7).

In general, T_b values were lowest during the day without flight action (BASE) and highest during the HANDLING (P<0.05) (V[u], Figure 8). During the days of aviation noise exposures, the T_b values of the vixens were highest before flight action decreasing from EXPO-1h to EXPO+1h (P<0.01), whereas during the day without exposure (BASE) T_b increased from EXPO-1h to EXPO+1h (P<0.01). T_b values were higher during the HANDLING period involving human activity, handling and transport than an hour before or after this period (P<0.05).
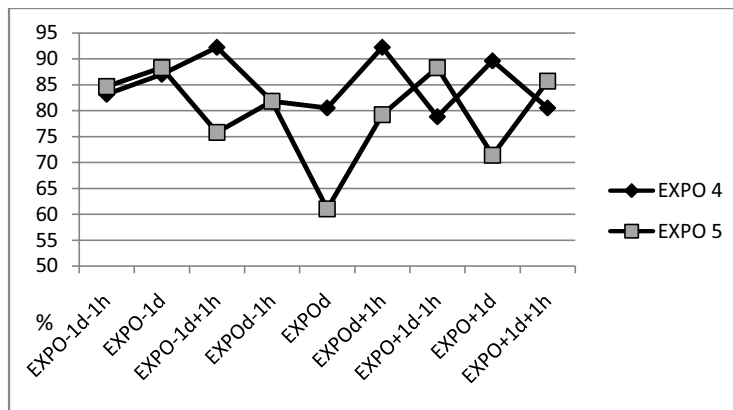
Figure 7. The percentages of observations vixens spent inside the nest during the periods of an hour before (-1h), the time of (EXPO), and an hour after (+1h) the noise exposure on the day before (EXPO-1d), on the day of (EXPOd), and on the day after (EXPO+1d) the noise exposures. Significances: flight (EXPO4 vs. EXPO5) P>0.1, day (EXPO-1d, EXPOd, EXPO+1d) P>0.1, period (EXPO-1h, EXPO, EXPO+1h) P>0.1, day*flight P>0.1, period*flight P<0.05, day*period P<0.1, day*period*flight P<0.05 (GLM for repeated measures, N=22).
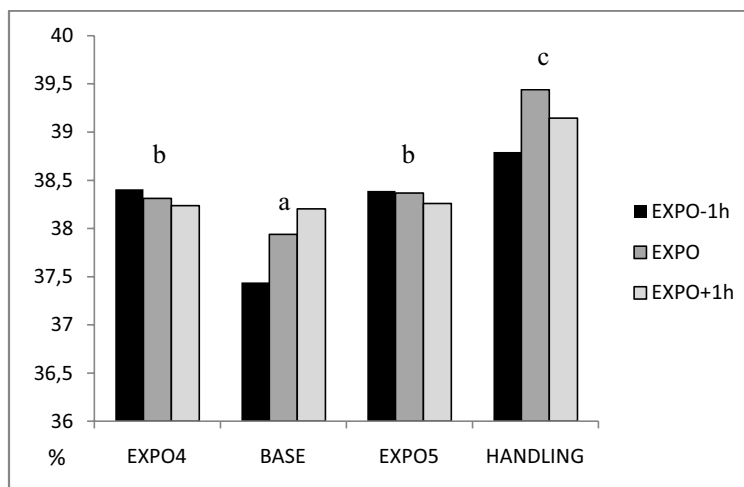
Figure 8. T_b (°C) of vixens during the day of the 4th noise exposure (EXPO4), on the day without noise exposure (BASE), on the day of the 5th noise exposure (EXPO5) and on the day of HANDLING An hour before (EXPO-1h), the time of (EXPO), and an hour after (EXPO+1h) the exposures. Statistically significant differences: Day P<0.05, interaction day*period P<0.01 (GLM for repeated measures). The exposures without a common letter differ at P<0.05 in the pair-wise comparison (N=10).

5.5 Reproductive success and management

Variation in the reproductive success and its subcomponents was high between years, between the experiments and between the experimental groups (I-V) (see Table 4). In general, the primiparous vixens had more failures or problems in reproduction than the multiparous vixens. Most of the problems in the primiparous vixens occurred at the beginning of the reproductive cycle, i.e., lack of oestrus and barrenness were the major problems. Moreover, cub losses were higher in the primiparous than in multiparous vixens (I, V). In general, litter size declined form birth to weaning, with the decline being greater in primiparous than in multiparous vixens (I, V). Of the dead cubs, 38 % disappeared, i.e., a reduction in the number of live cubs occurred during consecutive days of cub counting, and dead cubs were not found (V). Approximately 14 % of the dead cubs were stillborn, and 13% of all the dead cubs had bite wounds or were partly eaten (V). Generally, vixens ate the dead cubs if the dead cubs were not removed from the nest after death (I, II-V personal observation).

Unsupervised natural breeding in III was unsuccessful, as RPB was zero in both NB groups. Only one NB vixen in the enclosures whelped, but her cubs were destroyed within two weeks postpartum. In pair-housed vixens, better RPB and a higher percentage of vixens that succeeded in weaning their cubs was achieved with AI than with NB (III).

The body weight of the young vixens increased from September to November and decreased from November to March ($BM_1=7.9\pm1.0$ kg, $BM_2=12.1\pm1.8$ kg, $BM_3=10.7\pm 1.6$ kg, respectively, $P<0.05$, III[u]). BM_3 and ΔBM_{rel} were not observed to have an effect on the weaning success when the data of all vixens were pooled. However, in AI groups low BM_3 tended to have a positive effect on weaning success ($P=0.08$, Linear Mixed Models, Table 5). On the other hand, BM_3 and ΔBM_{rel} had no effect on the occurrence of oestrus, or the barrenness of the AI vixens ($P>0.1$, Linear Mixed Models). A lack of oestrus (or weak oestrus) seemed to be a problem in some families, as seven out of eight vixens without any signs of oestrous originated from the same two litters. Primiparous vixens with early selection and restrictive feeding had better RPM than traditionally

Table 4. Summary of the reproductive success and its subcomponents in the blue fox vixens for the experimental groups in studies I-V. PP=primiparous vixens, MP=multiparous vixens, HD=high housing density, LD=low housing density, SSE=stable social environment, AI-SC=artificially inseminated singly-housed vixens in a cage, AI-PC= artificially inseminated pair-housed vixens in cages, NB-PC=naturally bred pair-housed vixens with a male in cages, NB-PE =naturally bred pair-housed vixens with a male in enclosures. -=not analysed (See Table 2 for the groups)

Paper	Groups	RPB		RPM		Litter size		Cub losses %		No oestrus %		Barren %		Lost all %		Weaned %		Succeeded %	
		PP	MP	PP	MP	PP	MP	PP	MP	PP	MP	PP	MP	PP	MP	PP	MP	PP	MP
I	Video recorded	-	-	6.8	5.6	11.2	10.2	33	17	-	-	9	33	10	0	81	67	81	67
II	Control with HD	1.7	5.6	2.8	5.9	7.2	9.4	34	21	38	6	21	17	31	4	41	77	28	74
	LD with SSE	1.6	7.3	2.5	7.3	6.3	10.9	25	23	36	0	25	9	12	9	39	91	34	83
III	AI-SC	4.1	-	5.9	-	10.4	-	21	-	30	-	20	-	0	-	80	-	50	-
	AI-PC	1.3	-	2.1	-	8.0	-	54	-	42	-	25	-	8	-	67	-	25	-
	NB-PC	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	NB-PE	0	-	-	-	-	-	100	-	-	-	-	-	-	-	-	-	-	-
IV	Top nest	-	-	4.8	5.7	9.5	10.6	29	42	-	-	29	8	0	25	71	67	71	67
	Top and floor nest	-	-	4.9	5.5	9.3	8.1	17	23	-	-	27	6	9	28	64	67	64	67
V	Control	-	-	4.0	7.0	8.8	10.2	34	29	-	-	31	3	7	9	62	88	62	88
	Aviation noise	-	-	4.1	7.0	7.5	9.3	33	23	-	-	13	3	18	3	69	94	69	94

selected and fed vixens, achieving 5.5±3.6 and 3.6±3.6 cubs per mated vixen, respectively (P< 0.05, T-test) (V[u]).

Table 5. Body mass (kg) at the beginning of the breeding season (BM_3) and loss of body mass from December to March (ΔBM_{rel} %) for vixens with and without oestrus, for barren and whelped vixens and for successful and failed vixens in AI groups (III[u]). P_1 = difference in BM_3, P_2 = difference in ΔBM_{rel} (Linear Mixed Model).

Variable	BM_3	P_1	ΔBM_{rel}	P_2
No oestrous	11.6	P>0.1	5.0	P>0.1
Oestrus	10.9		10.0	
Barren	11.0	P>0.1	11.0	P>0.1
Whelped	10.9		9.0	
Failed	11.5	P<0.1	8.0	P>0.1
Succeeded	10.6		8.0	

6. DISCUSSION

Regulation of reproduction may occur throughout the reproductive season in farmed blue foxes. In this thesis, the effects of different treatments on reproductive success were assessed during various periods of reproductive cycle (see Table 1 in the literature review). Video recordings of maternal behaviour focused on the whelping period (I, V[u]). The aviation noise exposures occurred for the first time 0-35 days after insemination. Thus, the exposures could have affected implantation, pregnancy, whelping and maternal behaviour (V, V[u]). In II (some of the vixens), IV, V and V[u], the experimental treatments were started after insemination and continued until weaning. In contrast to these experiments, the treatments in the experiments focusing on the social environment (II, III) the treatments could have also affected oestrus and oestrus behaviour.

6.1 Maternal behaviour and infanticide

Infanticide (I, V) or lack of maternal behaviour (I) were not a common problem among blue fox vixens, not even after severe acute stressors (V). Both primiparous and multiparous blue fox vixens exhibited adequate maternal behaviour (I), despite moderate cub losses (I-V). These results are in accordance with previous studies based on direct observations or cub counting (Ilukha et al 1997, Sanson and Farstad 2003). Accordingly, the incidence of infanticide seems to occur less often in farmed blue foxes than in farmed silver foxes (Ilukha et al 2004; for silver foxes, see Braastad 1993, Braastad and Bakken 1993).

Infanticide among silver foxes seems to be of a social nature rather than due to factors related to barren housing environment (Bakken 1994). Low ranking silver foxes (Bakken 1994), as well as subordinates among wild red foxes (MacDonald 1980) are known to kill their own offspring due to social stress. After killing their cubs, subordinates generally help the dominant vixen to rear its cubs. Similarly, infanticidal low ranking silver fox vixens on farms, if given the opportunity, would help dominant vixens in rearing their offspring (Bakken 1993ab). Thus, infanticidal vixens may rely on the indirect route to genetic immortality by helping their relatives when they themselves are not able to breed (Stearns and Hoekstra 2000). This indirect strategy increases an

animal's inclusive reproductive fitness and chances of success in further reproduction. Generally, wild red fox vixens living in rather stable and predictable environments will have several new opportunities to reproduce themselves and would benefit from such a helping strategy.

Among wild arctic foxes, helping is not such a distinct phenomenon (Hersteinsson and Macdonald 1982, Moehlman 1989, Frafjord 1991, Strand et al 2000). In addition, postnatal reduction of litter size by arctic fox parents is not very likely either (Frafjord 1992a). Neither infanticidal behaviour (I), nor distinct helping behaviour in group housed foxes, whose reproductive success was diminished (III), were observed among farmed blue foxes in the experiments described in this thesis. It is probable that arctic foxes living in unpredictable environments and depending on fluctuating food resources, and having only one reproduction opportunity on average in their lifetime, regulate their reproduction in earlier phases of the reproductive period, i.e., oestrus, ovulation and early pregnancy, rather than with helping or infanticidal behaviour. The fact that the number of reproducing vixens and the number of cubs born are the main determinants of the reproductive rate in arctic foxes at a population level (Macpherson 1969, Bannikov 1970, Prestrud 1992c, Angerbjörn et al 1995) supports this hypothesis. Thus, it is probable that differences in the ecology of *V. vulpes* and *V. lagopus* may explain the observed differences in the occurrence of infanticidal behaviour and helping behaviour between farmed silver and blue foxes. Therefore, the behavioural differences between these two species should be taken into account when developing new or alternative farming practices for farmed foxes.

The lack of infanticidal behaviour in farmed blue fox vixens might indicate that no major behavioural problems can be expected to occur under present farming conditions during the breeding season. However, it might also be possible that infanticidal behaviour is not included in the reproductive strategies of *V. lagopus*. Thus, the lack of infanticidal behaviour *per se* on farms does not mean that the farm environment would not be stressful for the foxes; rather, part of the heat problems and barrenness, i.e., problems earlier in the breeding season, may represent responses to stress.

6.2 Social environment

Even though the social environment is known to affect reproduction in small canids (Geffen et al 1996), the social environment of farmed foxes is often manipulated (Harri et al 1999), with changes accumulating during the most vulnerable period, the breeding season. In contrast to farmed blue foxes, which are relocated several times before and after insemination, wild arctic foxes have established their territories, dens and mates well before breeding (Chesemore 1975, Audet et al 2002). Accordingly, in the domestic environment, animals are grouped and forced to interact with each other in ways that may be rather different from the natural conditions for which their social behavioural patterns have evolved (cf. Hart 1985).

Likewise wild arctic fox males (Frafjord 1991) farmed blue fox males also take part in feeding, guarding and playing with cubs (Malm 1995). In the present thesis, the importance of males in cub care within a group could not be assessed, since no cubs survived until the emergence from dens in NB groups (III). Whether the reproductive failures resulted from the females or from the males' mating or fertilizing capability, is impossible to say, as in this study the functioning of testis was not assessed in these yearling males. In farmed blue foxes, older males of higher rank are known to socially displace the younger ones (Korhonen and Niemelä 1993) and affect on the mating willingness in the yearling males due to social pressure (see Farstad 1998). Therefore, it may be possible that pheromones from other parts of the farm from older or more dominant males may have affected the willingness of these inexperienced males to mate. In general, reproductive failures are seldom caused by the breeding males, because breeding males and their semen quality are carefully inspected before insemination (Pylkkö et al 2005). Moreover, young males are often used for only a few vixens during their first breeding season to ensure that the semen production is sufficient to consistently yield good quality semen.

According to previous studies, reproductive success in group housed silver and blue foxes generally seems to be either unaffected or reduced (Kullberg and Angerbjörn 1992, Korhonen et al 1994, 1997, Pedersen 1997, Pyykönen et al 1997, 2002b). In the present thesis, naturally bred, group housed vixens totally failed to reproduce (III), and group housed AI vixens tended to have lower RPM than single-housed vixens. These

results are in accordance with previous studies in seminatural environments where the reproduction success has been inferior to traditional farm situations (Kullberg and Angerbjörn 1992, Korhonen and Alasuutari 1994). In groups of three vixens of different age with a male or several males in seminatural conditions, only 22 % of the vixens succeeded in weaning their cubs (Korhonen and Alasuutari 1994), while only one cub was weaned in groups of two and three vixens and a male (Kullberg and Angerbjörn 1992). In both these studies, only dominant vixens in a group succeeded in reproducing. These dominant vixens were also observed to display assertions of dominance to subordinate females which may have suppressed the reproduction of subordinates.

The present results show that the effects of social environment on reproductive success remains somewhat unclear, as no statistically significant results in RPM or RPB or their subcomponents were found between stable and unstable social environments with low and high animal densities (II). However, pair-housing of female siblings tended to have a negative effect on reproductive success, while single housing in every second cage with stable social environment (SSE) provided the best reproductive success in primiparous vixens (III). In SSE, animals were not moved to new cages during the breeding season, and it is therefore possible that the reproductive success may have been affected by the social environment and animal-animal relations. On the other hand, it is impossible to say whether RPM was positively affected only by SSE itself or whether the low level or even the type of human handling may have affected the results. The highest T_b values were observed during the periods of human activity and handling (V^u), thus indicating that the animals experienced stress due to human proximity. Therefore, T_b may be a better indicative of stress level than reproduction effects. It is also possible that the effects of social environmental on reproduction are subtle and mostly affect the offspring during their life, i.e., stress experienced by the pregnant vixens may affect the development of their offspring (see e.g., Osadchuk et al 2001, 2003ab).

Nests with a tunnel entrance, which have been shown to have positive effects on reproductive success in blue foxes (Haapanen et al 1990), were used in III. The availability of a tunnel nest may have improved the reproductive results in the vixens that whelped. On the other hand, because the number of animals in these studies (II, III)

was quite low and standard deviations high, type two errors may have occurred in the results.

6.3 Nests

In the wild, arctic foxes prefer to use the same dens season after season, and the use of multiple dens is characteristic for this species (Anthony 1996). In addition, artic fox dens are often situated at high elevations and form complex structures with several entrance tunnels (Audet et al 2002). Two nests were recommended for farmed foxes already in the 1930s (Broberg and Puustinen 1931). However, in practice, blue fox vixens are still provided with only one nest just some two weeks before their expected whelping. In addition, the nests used generally comprise a wooden two-roomed floor nest with only one entrance. Modified nests, e.g., top nests (silver foxes: Pyykönen et al 2004, blue foxes: Mononen et al 1999, both species: Jeppesen & Pedersen 1990) and tunnel nests (silver foxes: Braastad 1994, blue foxes: Moss & Östberg 1985, Haapanen et al 1990) have been shown to have positive effects on the reproduction of both silver and blue foxes, and especially for primiparous vixens. Therefore, in some of the experiments of this thesis vixens were provided with a tunnel nest (I, III) or either with a top nest or a top nest together with a traditional floor nest (IV).

Although not studied *per se,* the present thesis with previous scientific data suggests that a nest with tunnel entrance would be beneficial for primiparous vixens. This was demonstrated by the high RPM achieved with tunnel nests (5.9 cubs, III). This RPM was the same or even higher than the average national RPM for the same year using traditional housing conditions (RPM= 3.9 cubs for primiparous vixens and 5.6 cubs for both primi- and multiparous blue foxes, Smeds, unpublished data).

RPM in primiparous vixens was as good in the vixens housed with a top nest only as in those that had both floor and top nest in use (IV). RPM in IV was similar to the national average of the same year in Sampo farms (3.9 cubs, Smeds, unpublished data). These results suggest that either a top nest alone or top nest with an additional nest are suitable for primiparous blue fox vixens.

On the other hand, multiparous vixens generally had lower RPM (5.6 cubs) in both the group with a top nest and the group with two nests (IV) than the national average in the same year for multiparous vixens in Sampo farms (7.6 cubs, Smeds unpublished data). Given the opportunity to choose between the two nest types, the multiparous vixens favoured the top nest for whelping, in contrast to primiparous vixens, which chose the familiar floor nest (IV). The choice of multiparous vixens was surprising because multiparous vixens had no earlier whelping experience with the top nests, and early experiences have been shown to affect animals' later preferences and behaviour (Broom and Johnson 1993). The multiparous vixens' option of choosing between nests was reflected in the lower cub losses for the group with two nests than for that with a top nest only. For some reason, vixens seem to prefer one nest over another, even if the nests are identical (Broberg and Puustinen 1931). It is likely that two nests might increase foxes' control over their living environment within the cage. The awareness of the additional, and in this case familiar nest, might have made these vixens feel more secure, as they had the possibility of transferring their cubs to the familiar nest (IV). The present results indicate that two nests may provide foxes with a better sense of control and reduce stress, thereby increasing reproductive success (cf. Broom and Johnson 1993).

The present results reveal that multiparous vixens should not be suddenly provided with a new nest type but should instead be habituated to an unfamiliar nest together with a familiar nest, if the nest type is going to be changed on farm. Primiparous vixens, on the other hand, seem to reproduce as well even in unfamiliar nest types, even though they may prefer the one they have been born in. The possibility of using two nests was exploited in the present study, with nearly half of the vixens moving their cubs from one nest to another at least once during the two postpartum weeks. In addition, two vixens split their litters between the two nests. Such behaviour resembles the behaviour of the blue fox's wild relatives, with the exception that the transferring of cubs in farmed foxes occurred earlier (soon after birth) in this study than has been reported in the arctic fox (Frafjord 1992a).

Similarly to previous studies (Moss and Östberg 1985, Haapanen et al 1990, Mononen et al 1999), the present study suggests that more complicated nest types containing key features of the natural dens of the arctic fox (e.g., several entrances, complicated

structure, and elevated location) would increase the reproductive success of primiparous blue fox vixens (III, IV). It is possible that such nests would enable better control over the nest than simple floor nests and would therefore also have positive effects on foxes' welfare. However, it may be questioned whether the farmed foxes should be provided with more complicated nests, which could be used by the fox for hiding and avoiding human contact, which can readily lead to feralisation (see Ahola 2002). Indeed, nests that are provided throughout the year have been shown to increase blue foxes' fear towards humans (Harri et al 1997, 1998b, Korhonen et al 2006). Therefore, if avoidance of humans is possible due to housing conditions, greater attempts should also be made to habituate foxes to humans. Such attempts could include early handling of foxes (e.g., Pedersen 1991, 1992, 1993b, 1994), habituating fox cubs to the farm environment by using nests with transparent wire netting front wall (Pedersen 1991), selection for more confident animals for breeding (e.g., Belyaev et al 1985, Rekilä et al 1997, Rekilä 1999, Nikula et al 2000, Kenttämies et al 2002) and reducing foxes' fear of humans by giving them positive rewards (Dale and Bakken 1992, Bakken et al 1993, Bakken 1998). On some farms, farmers give the vixens that whelp late in a season (when the outdoor temperature is higher) a nest without a roof, i.e., open nests. This arrangement is rather similar to the nest with a transparent front wall (Pedersen 1991) and also enables vixens to observe the farm environment to all directions without leaving the cubs. In addition, it increases human animal contacts and habituates the cubs early to humans.

6.4 Acute stressors: aviation noise and handling

It is known that acute stress may cause reduced reproduction (Moberg 2000). Lactating females, however, are buffered against disturbing physical and emotional stimuli, thus making the adrenal secretor response caused by physical or emotional stimuli smaller in lactating than in non-lactating females (Stern and Levine 1972 in Hart 1985). It is likely that this phenomenon may have also affected the response of the pregnant and lactating blue fox vixens in the present study, as severe acute aviation noise exposures were not observed to cause cub killing or a reduction in reproductive success (V). If the noise exposures had occurred during oestrus development or ovulation, these noise exposures might have had a negative effect on reproductive success, since ovulation is especially sensitive to stress (Moberg 2000). In addition, for successful ovulation, an exact timing between pre-ovulatory releases of the luteinizing hormone is needed to induce ovulation

and the expression of oestrus behaviour (Moberg 2000), and this critical biological event may be blocked by an acute stressor causing distress. It is also possible that the noise exposures were not stressful enough to cause a severe stress reaction leading to reduced RPM.

The aviation noise exposures caused no major changes in foxes' daily behaviour (V^u). During the 5th noise exposure, however, vixens briefly decreased their time spent inside the nest. These vixens were mostly primiparous vixens, which are known to be more restless before and after whelping than multiparous vixens (I), and therefore probably reacted more strongly to the aviation noise. In addition, the primiparous vixens that spent more time outside the nest during the noise exposure also spent more time outside the nest during the following day at the same time. At that time, the additional vixens that were used for the T_b measures were removed from the farm. It is likely that the primiparous vixens reacted to the human activity which was evidently needed when transporting the additional foxes. This supports the idea that primiparous vixens are more sensitive to aberrant happenings and more easily react to new stimuli.

Other experiments concerning the effects of aviation noise on reproduction in farmed foxes are scarce. Mononen et al (2003) found that reproductive success was not related to the behaviour of vixens during aviation noise exposures, since fearful (30 % of the animals), alert (43 %) and passive (28 %) vixens reproduced similarly. The high inter-individual variation in behaviour as a response to aviation noise indicates that single individuals perceive aviation noise differently, with some foxes perceiving it highly aversive. In the silver fox, the behavioural responses to flying aircraft have been reported to be minimal (Braastad and Bakken 1993). In contrast, both silver and blue foxes have been reported to respond to noise exposure, though the effects of the humans involved in the experimental procedure and the response to the noise could not be distinguished (Mononen and Harri 1991).

Acute stressors such as restraint and transportation have been found to disrupt the events surrounding ovulation (Moberg 2000). However, in my study, good RPM was also attained with traditional farming routines, which include both restraint and transportation, i.e., vixens were moved from cage to cage before and after insemination (I, V). Similar routines are also used by several top farmers in Finland with good

success (Finne 1996ab). This may indicate that there are still other more important factors than simple acute environmental stressors that may affect RPM because of its multifactorial character. It is obvious that physiology, e.g., health, body condition and heredity, of the breeding foxes plays an important role in reproductive success as well as the care taken by the farmer in dealing with farming routines (e.g., Sanson and Farstad 2003, AI: Jalkanen and Joutsenlahti 1988).

In the present study, physiological reactions, i.e., changes in body temperature, to acute stressors were assessed in non-breeding vixens. Deep body temperatures were higher during handling than during noise exposures and lowest during the period without acute stressors. This indicates that for blue foxes handling (human activity) and relocating foxes in random social order is more stressful than acute aviation noise exposures. In silver foxes, the presence of humans and other silver foxes has been reported to result in SIH whereas recorded loud noises not (Bakken et al 1999). In farmed blue foxes, Harri et al (2000) found that SIH and activity of foxes were not affected by either the presence of an unknown human (standing still) for one minute, or measurement of rectal temperature. However, introducing an unknown fox to the experimental foxes caused a high rise in SIH, heart rate and activity. These results are in accordance with the results of the present study which indicate that human activity results in increased T_b values in blue foxes. In the present thesis, T_b values were highest an hour before the aviation noise exposures during the time when human activity was at its highest on the farm, for example, when cubs were counted, animals fed or the experimental set up was checked. T_b values decreased from hour to hour and were at their lowest an hour after the exposures, after the people had left the farm.

In conclusion, acute aviation noise exposures do not seem to impair the reproductive success of blue fox vixens, nor do they increase cub losses or cub killing (V). However, noise exposures cause SIH in the foxes and may reduce the time spent with cubs in some vixens, and can therefore be considered a stressor (V^u). On the other hand, human activity and handling also cause raise in SIH, indicating that human animal relations and the way animals are handled are of great importance in terms of animal welfare.

6.5 Management

High variation in RPM and its subcomponents were observed in the experiments of this thesis and between years. In practice, there is also high variation in RPM between farms (Smeds 1992). This variation between the farms is most likely due to differences in these farms' fox populations resulting from different bases for selection, such as fur quality, body size or fertility. In addition, variation in RPM between farms may result in the management routines used. In the present study, the studied treatments did not have a clear effect on RPM or its subcomponents. Therefore, it can be assumed that no single environmental factor that the animals were exposed to during the current studies may strongly affect reproductive performance (or animal welfare). It is more likely that other factors not studied in this thesis, and related to the domestic environment may have a greater effect on reproductive success. Later or delayed effects, i.e., impaired reproductive success at maturity on cubs of vixens exposed to stress during pregnancy (e.g., Osadchuk et al 2001, 2003ab), were not assessed in this thesis, but may be of significance.

In the present thesis, the effect of management, including early selection with early restricted feeding (V^u) and the breeding system (AI vs. NB) was assessed (III, III^u). In addition, the correlation between reproductive success and breeding weight of vixens was evaluated (III^u). The results revealed that early selection of young breeding blue fox vixens followed by restricted feeding led to an increase in RPM (V^u). Moreover, low body mass at the beginning of the breeding season tended to have a positive effect on the percentage of successful vixens in AI vixens (III^u) which is in accordance with Sanson and Farstad (2003).

Since farmed blue foxes have retained the ability for extreme body fat deposition (Nieminen et al 2004), overfeeding and fat accumulation can lead to extreme obesity, which is detrimental to the reproductive success of farm bred foxes (Broberg and Puustinen 1931, Fougner 1991, Sanson and Farstad 2003, Nieminen et al 2004). Despite the known negative effects of overfeeding, the breeding animals are probably selected too late and overfed on many fur farms. Selection of young breeding animals and restricted feeding should take place in early autumn to avoid overfeeding and fat accumulation (Koskinen et al 2007). Generally, young blue foxes weigh 6-8 kg already

in September (FFBA 1998), as was also observed in the present study (III^{II}). At the time of selection (November-December), young breeding vixens may weigh up to 20 kg. Thereafter, their body mass should be decreased by more than 50 % to reach the ideal breeding weight of 6-8 kg (Sanson and Farstad 2003). Although food deprivation during winter seems not to have any effect on estradiol and progesterone concentrations in blue fox vixens (Nieminen et al 2004), food deprivation and extreme weight loss may be very stressful for vixens. However, it is probable that even after such a severe loss of body weight, vixens will still be too fatty for breeding, thus diminishing their reproductive success. Therefore, it is possible that management problems, such as overfeeding of young vixens and overweight at its reflection, could override the positive effects of more complicated nests and a stable social environment. This may have led to the erratic results and conclusions drawn in this thesis, as well as in other studies concerning the reproduction and welfare of farmed foxes.

A lack of oestrus in the first breeding season is inheritable and seems to be becoming increasingly common among blue fox vixens (Pylkkö et al 2005). In the present study, more than 35 % of the primiparous vixens showed no signs of oestrus (II, III), most of them originating from the same litters (III). Thus, vixens showing problems with oestrus development in their first breeding season should not be selected for use as breeding stock unless the breeding goal is to have a breeding stock where vixens breed for the first time at the age of two years.

Artificial breeding has led to problems in animal reproduction (Hart 1985). For example, less attention has been devoted to the details of sexual interactions between males and females, both of which may have problems in normal reproduction. Animals not displaying the full range of sexual behavioural patterns in a domestic environment have still been able to reproduce with the help of humans. Concerning fox males, it is possible that the common use of AI on farms has effectively selected males of a large body size, high fur quality and tame character, which assure easy semen collection for artificial breeding. Such males represent the optimal breeding type and ensure the economical efficiency of the breeding. Concurrently, some other characteristics, including the desire to copulate may have been partly selected out, which may have been the reason for the low reproductive success observed in NB groups (III). On the other hand, the quality of the semen in NB males was not studied, and it might therefore

be possible that these males (or some of them) were infertile. In pair-housed vixens, better RPM was achieved with artificial insemination than with unsupervised natural breeding (III). This indicates that, indeed, the use of artificial breeding has led to blue fox populations that reproduce best artificially with the help of humans.

Human-animal relations are known to be highly important for animals' welfare (e.g., Waiblinger et al 2006). The T_b measurements in this thesis indicate that human activity and handing are the most stressful stimuli experienced by foxes in their domestic environment. Therefore, it is important to place more attention on positive human-animal relations and to habituate foxes to handling and farming routines, as has earlier been suggested by Pedersen (1991). Positive and more predictable handling can reduce stress, thereby leading to increased reproduction (e.g., Ladevig 1991, Broom and Johnson 1993). Selection of confident behavior is an effective way to reduce the stress experienced by foxes in human proximity (Belyaev et al 1985, Rekilä 1999, Rushen et al 1999) as well as increase the welfare of farmed blue foxes. Selection of more confident vixens (Rekilä 1999, Kenttämies et al 2000, 2002) together with positive handling provide more trusting breeding animals, whose cubs learn trusting behaviour from their mothers (Harri et al 2003).

Vixens can be quickly habituated to the checking of nests (personal observation). In the present thesis, the experimental vixens were conditioned to leave their nests after knocking on the nest for the time their cubs were counted. Foxes learned this procedure rapidly. Similarly, breeding animals could be habituated to loud noises and human activity. If foxes are habituated to human handling, for example, by checking nests and cub counting, it becomes easier to handle the animals and assist during whelping if necessary. From the farmers' point of view, regular inspection of nests ensures reasonable book keeping and documentation for breeding animal selection. Moreover, in the case of possible compensation applications of suspected cub losses (e.g., due to low quality feed, over flights or noise from chopping machines) regular counting of cubs can provide proper documentation of cub losses.

In summary, RPM or its subcomponents in blue fox vixens was little affected by any single environmental factor. However, factors related to management seemed to have a greater effect on reproductive success. Therefore, the barren farm environment can not

solely be blamed for the reproductive failures of blue foxes, particularly in light of the excellent reproductive success attained annually by some farmers despite the use of a barren cage environment. Thus, farmers' management skills and their skills in handling animals are of great importance. It has been previously shown that farmers attitude towards their animals can greatly affect animal welfare and that this attitude can be trained in a better direction (e.g., Hemsworth 2002). Improving farmers' professional skills and attitudes towards farming could provide the most rapid means of improving the welfare of farmed blue foxes.

Indeed, although much scientific knowledge about fur animals and their farming is available, the link between science and practice and *vice versa* has been insufficient. Therefore, it would be worth the effort to discuss the management problems with the farmers and to find answers to their questions with the help of research, not to mention the practical trials of new methods tried out by farmers, the importance of which should be scientifically proved.

7.   CONCLUSIONS

The present study demonstrated that environmental factors have little effect on the reproduction of farmed blue foxes. The results reveal the following conclusions:

1. Infanticide is not a common problem in blue foxes. Cub mortality from birth to weaning may, however, be moderate. Early cub losses represent approximately 80 % of the losses and are seldom observed by the farmers. Postnatal cub losses are higher in vixens that whelp for the first time than in experienced vixens.

2. The periparturient behaviour of primiparous vixens is similar to that of multiparous vixens, although primiparous vixens are probably more restless during the last day before and the first three days after whelping than are multiparous vixens. Generally, vixens spend most of their daily time with their newborn cubs, most of which is spent resting and providing the cubs with warmth and nutrition.

3. Major reproductive failures in blue foxes include the lack of oestrus, week oestrus, barrenness and losses of entire litters. These failures together account for up to 50 % of the failures in the primiparous breeding vixens. These failures are less frequent in multiparous vixens. Variation in reproductive success between years can be quite notable.

4. Low housing density and especially stable social environment may improve the reproduction in singly-housed blue foxes. The presence of supplemental vixens in the same cage or enclosure seems to impair reproduction of blue foxes.

5. Nests having some key features of natural dens of *Vulpes lagopus*, such as a tunnel and top nest, seem to be appropriate for blue foxes, especially for primiparous vixens. In addition, vixens readily use an additional nest if given the option. An unfamiliar nest may increase cub losses in the litters of multiparous vixens, particularly if the unfamiliar nest type is the only nest available.

6. Aviation noise during pregnancy and the lactating period does not seems to reduce reproduction or cause cub killing. Human presence and handling seem to be more stressful for foxes than severe noise exposures. Therefore, it is important in terms

of animal welfare to habituate foxes to human handling and select timid animals for breeding.

7. More attention should be focused on management in general, and especially on the management of feeding throughout the year. Early selection of young breeding vixens and restricted feeding after reaching adult size (in September-October) increase reproductive performance and are highly recommended.

8. Improvement of management and human-animal relations might be the best ways to improve reproductive performance and welfare of farmed blue fox vixens. Thus, more research is needed to define basic management problems and the needs of breeding foxes. In addition, actions increasing co-operation between research and practice are highly recommended.

8. REFERENCES

Ahola L: Effects of Social and Physical Housing Environment on the Welfare in Silver Foxes (*Vulpes vulpes*). Kuopio University Publications C. Natural and Environmental Sciences 145, 2002

Ahola L, Harri M, Mononen J, Rekilä T: Family housing of blue and silver foxes in a row cage system. In: Frindt A, Brzozowski M (Eds): Applied Science Reports 29. Progress in fur animal science. Proceedings from the VI International Scientific Congress in Fur Animal Production, 21-23 August 1996, Warsaw, Poland, pp 71-76. Polish Society of Animal Production, 1996

Alcock J: Animal behaviour. An evolutionary approach. 6th edition, Sinauer Associates, Inc., Sunderland, Massachusetts, USA, 1997

Angerbjörn A, Arvidson B, Norén E, Strömgren L: The effect of winter food on reproduction in the arctic fox, *Alopex lagopus*: a field experiment. Journal of Animal Ecology 60: 705-714, 1991

Angerbjörn A, Tannerfeldt M, Bjärvall A, Ericson M, From J, Norén E: Dynamics of the arctic fox population in Sweden. Annales zoologici Fennici 32: 55-68, 1995

Angerbjörn A, Hersteinsson P, Tannerfeldt M: Arctic fox *Alopex lagopus* (Linnaeus, 1758). In: Sillero C, Hoffmann M, Macdonlad D.W (Eds.): Canids: foxes, wolves, jackals and dogs. pp 117-123, IUCN/SSC Canid Specialist Group. Gland, Switzerland and Cambridge, UK, 2004

Anthony RM: Den use by arctic foxes (*Alopex lagopus*) in a subarctic region of western Alaska. Canadian Journal of Zoology 74: 627-631, 1996

Anthony RM, Barten NL, Seiser P: Foods of arctic foxes (*Alopex lagopus*) during winter and spring in western Alaska. Journal of Mammalogy 81: 820-828, 2000

Arvidson BE, Angerbjörn A: Kannibalism bland fjällrävsvalpar? Viltnytt 24: 27-33, 1987

Audet AM, Robbins CB, Larivière S: *Alopex lagopus*. Mammalian Species 713: 1-10, 2002

Bakken M: The relationship between competition capacity and reproduction in farmed silver fox vixens, *Vulpes vulpes*. Journal of Animal Breeding Genetics 110: 147-155, 1993a

Bakken M: Reproduction in farmed silver fox vixens (*Vulpes vulpes*), in relation to own competition capacity and that of neighbouring vixens. Journal of Animal Breeding and Genetetics 110: 305-311, 1993b

Bakken M: Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*. Dr. Scient. Avhandling. Zoologisk Institutt, Det Matematisk-Naturvitenskapelige Fakultetet, AVH, Universitetet Trondheim, 1994

Bakken M: The effect of an improved man-animal relationship on sex ratio in litters and on growth and behaviour in cubs among farmed silver fox (*Vulpes vulpes*). Applied Animal Behaviour Science 56: 309-317, 1998

Bakken M, Moe R, Smith A: Radio telemetry: a method of evaluating stress and leaning ability in the silver fox (*Vulpes vulpes*). Proceedings of the International Congress of Applied Ethology, 26-30 July, Berlin, Germany, pp 591-594, 1993

Bakken M, Braastad BO, Harri M, Jeppesen LL and Pedersen V: Production conditions, behaviour and welfare of farm foxes. Scientifur 18: 233-248, 1994

Bakken M, Moe RO, Smith AJ, Selle GME: Effects of environmental stressors on deep body temperature and activity levels in silver fox vixens (*Vulpes vulpes*). Applied Animal Behaviour Science 64: 141-151, 1999

Bannikov AG: Arctic fox in the USSR: biological premises of productivity. International Union for Conservation and Nature and Natural Resources, Publications New Series 16: 121-130, 1970

Bazer FW, Clawson AJ, Robison OW, Ulberg LC: Uterine capacity in gilts. Journal of Reproduction and Fertility 18: 121, 1969

Belyaev DK, Plyusnina IZ, Trut LN: Domestication in the silver fox (*Vulpes fulvus desm*): changes in physiological boundaries of the sensitive period of primary socialisation. Applied Animal Behaviour Science 13: 359-370, 1985

Boivin X, Le Neindre P, Garel JP, Chupin JM: Influence of breed and rearing management on cattle reactions during human handling. Applied Animal Behaviour Science 39: 115-122, 1994

von Borrel E, Dodson H, Prunier A: Stress, behaviour and reproductive performance in female cattle and pigs. Hormones and Behaviour 50: 130-138, 2007

Boue F, Delhomme A, Chaffaux S: Reproductive management of silver foxes (*Vulpes vulpes*) in captivity. Theriogenology 53: 1717-1728, 2000

Braastad BO: Periparturient behaviour of successfully reproducing farmed silver-fox vixens. Applied Animal Behaviour Science 37: 125-138, 1993

Braastad BO: Reproduction in silver fox vixens in breeding boxes with and without an entrance tunnel. Acta Agriculturae Scandinavica Section A Animal Science 44: 38-42, 1994

Braastad BO: Behaviour of silver foxes in traditional breeding boxes and in boxes with an entrance tunnel. Animal Welfare 5: 155-166, 1996

Braastad BO, Bakken M: Maternal infanticide and periparturient behaviour in farmed silver foxes *Vulpes vulpes*. Applied Animal Behaviour Science 36: 347-361, 1993

Braastad BO, Osadchuk LV, Lund G, Bakken M: Effects of prenatal handling stress on adrenal weight and function and behaviour in novel situations in blue fox cubs (*Alopex lagopus*). Applied Animal Behaviour Science 57: 157-169, 1998

Brambell Committee: Command Paper 2836. Report of the Technical Committee to enquire into the welfare of animals kept under intensive livestock husbandry systems. Her Majesty's Stationery Office, London, 1965

Broberg A, Puustinen V: Tärkeimmät turkiseläimet ja niiden hoito. Werner Söderström Osakeyhtiö, Finland, 1931

Bronson FH: Mammalian Reproductive Biology. Chicago: Chicago University Press, 1989

Broom DM, Johnson KG: Stress and Animal Welfare, 1st edition. Chapman & Hall, London, 1993

Chesemore DJ: Den ecology of the arctic fox in northern Alaska, Canadian Journal of Zoology 47: 121-129, 1969

Chesemore DJ: Ecology of the arctic fox (*Alopex lagopus*) in North America – a review. In: Fox MW (Ed.): The wild canids, their systematics, behavioural ecology and evolution, pp 143-163. 1st edition. Van Nostrand Reinhold, New York, USA, 1975

Chirkova AF, Kostyaev LM, Rybalkin V: Peculiarities of the trapping and biology of Arctic Fox on south-western coast of the Kara Sea in winter, 1956-57. Proceedings of All-Union Institute of Animal Material and Furs 18, 1959

Clubb R, Mason GJ: Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Applied Animal Behaviour Science 102: 303-328, 2007

Dalerum F, Tannerfeldt M, Elmhagen B, Becker D, Angerbjörn A: Distribution, morphology and use of arctic fox *Alopex lagopus* dens in Sweden. Wildlife Biology 8: 185-192, 2002.

Dale OK, Bakken M: Ein dagleg godbit skader ikkje. Ein metode til å betre forholdet mellon rev og røkter. Norsk Pesdyrblad 66: 13-16, 1992

Day CS, Galef BG: Pup cannibalism: One aspect of maternal behaviour in golden hamsters. Journal of Comparative Physiology and Psychology 91: 1179-1189, 1977

Duncan IJH, Fraser D: Understanding animal welfare. In: Appleby MC, Williams DA, lynch GS (Eds): Animal welfare, pp 19-31, CAB International, Wallingford, UK, 1997

Eberhardt LE, Garrott RA, Hanson WC: Den use by arctic foxes in Northern Alaska. Journal of Mammalogy 64: 97-102, 1983

Einarsson E, Skrede A: Avl og föring av rev. Landbruksforlaget. Engers Boktrykkeri A/S, Otta, 1989

European Convention: Standing Committee of the European Convention for the protection of animals kept for farming purposes. Recommendations concerning fur animals. T-AP (96) 19, 1999

European Commission: The Welfare of Animals kept for Fur Production. Report of the Scientific Committee on Animal Health and Animal Welfare. Available in the Internet: http://ec.europa.eu/food/fs/sc/scah/outcome_en.html Adopted 28.08.2008, 2001

Farm Animal Welfare Council (FAWC): Second report on priorities for research and development in farm animal welfare. FAWC, Ministry of Agriculture, Fisheries and Food, Tolworth (Now DEFRA, London). Available on the Internet: http://www.fawc.org.uk/freedoms.htm Adopted 28.08.2008, 1993

Farstad W: Reproduction in the blue fox vixens (*Alopex lagopus*) In: Tauson AL, Valtonen M (Eds.): Reproduction in carnivorous fur bearing animals. Nordic Association of Agricultural Scientists. Report 75, p. 119-133, Copenhagen, Denmark, 1992

Farstad W: Reproduction in foxes: current research and future challenges. Animal Reproduction Science 53: 35-42, 1998

Fine H: Ecology of arctic foxes at Prudhoe Bay, Alaska. MSc thesis, University of Alaska, Fairbanks, 1980

Finne L: Näin meillä tehdään... Turkistalous 10: 267-271, 1996a

Finne L: Näin meillä tehdään…Turkistalous 11: 290-91, 310, 1996b

Finnish Fur Breeders' Association: Siniketun pentujen painonkehitys. (Development of body mass in blue fox cubs). Turkistalous 8: 225, 1998

Finnish Fur Breeders' Association: Statistics. Turkistalous 8: 33, 2007a

Finnish Fur Breeders' Association: Statistics. Turkistalous 6: 5, 2007b

Finnish Fur Breeders' Association: Turkistiloilla tuotettujen ketunnahkojen maailmantuotos / tarjonta. Turkistalous 8: 33, 2007c

Finnish Fur Breeders' Association: Ravintoainesuositukset 2007. http://www.stkl-fpf.fi/modules/system/stdreq.aspx?P=59&VID=default&SID=213921969388321&S=0&C=24861 Adopted 28.08.2008, 2007d

Finnish Fur Breeders' Association: Breeding. Available in the Internet: http://www.stkl-fpf.fi/modules/system/stdreq.aspx?P=37&VID=default&SID=431898424415859&S=0&C=19529 Adopted 16.10.2008, 2008a

Finnish Fur Breeders' Association: Fur animal feed. Available in the Internet: http://www.stkl-fpf.fi/modules/system/stdreq.aspx?P=38&VID=default&SID=988946138317121&S=0&C=23408 Adopted 3.11.2008, 2008b

Fougner JA: Valpedödlighets problematikken hos blårev. Norsk Pelsdyrblad 65: 6-10, 1991

Fougner JA: Artificial insemination in fox breeding. In: Tauson AL, Valtonen M (Eds.): Reproduction in carnivorous fur bearing animals. Report 75, pp 146-152, Nordic Association of Agricultural Scientists, Copenhagen, Denmark, 1992

Frafjord K: Fjellrevens (*Alopex lagopus*) atferd i hionrådet. Cand Real Thesis, University of Trondheim, Trondheim, 1984

Frafjord K: Adult arctic foxes *Alopex lagopus* L. in the denning area; numbers and behaviour. Fauna Norvegica Series A 12: 41-48, 1991

Frafjord K: Denning behaviour and activity of arctic fox *Alopex lagopus* pups: Implications of food availability. Polar Biology 12: 707-712, 1992a

Frafjord K: Behavioural ecology and behavioural energetics in the arctic fox *Alopex lagopus*. Dr. Scient. Thesis, University of Bergen, Bergen, 1992b

Frafjord K: Reproductive effort in the arctic fox *Alopex lagopus*: a review. Norwegian Journal of Agricultural Sciences 7: 301-309, 1993a

Frafjord K: Agonistic behaviour and dominance relations of captive arctic foxes (*Alopex lagopus*) in Svalbard. Behavioural Processes 29: 239-252, 1993b

Frafjord K, Becker D, Angerbjörn A: Interactions between arctic and red foxes in Scandinavia, predation and aggression. Arctic 42: 354-356, 1989

Fraser D, Weary DM, Pajor EA, Milligan BN: A scientific conception of animal welfare that reflects ethical concern. Animal Welfare 6: 187-205, 1997

Fuglei E, Mustonen AM, Nieminen P: Effects of season, food deprivation and re-feeding on leptin, ghrelin and growth hormone in arctic foxes (*Alopex lagopus*) on Svalbard, Norway. Journal of Comparative Physiology B 174: 157-162, 2004

Garrot RA, Eberhardt LE: Mortality of arctic fox pups in northern Alaska. J Mammal 63: 173-174, 1982

Garrot RA, Eberhardt LE: Arctic fox. In: Novak M, Baker JA, Obbard EE, Malloch B. (Eds.): Wild Furbearer Management and Conservation in North America, pp 395-406, Ministry of Natural Resources, Ontario, 1987

Garrot RA, Eberhardt LE, Hanson WC: Summer food habits of juvenile arctic foxes in northern Alaska. Journal of Wildlife Management 47: 540-545, 1983a

Garrot RA, Eberhardt LE, Hanson WC: Arctic fox den identification and characteristics in northern Alaska. Canadian Journal of Zoology 61: 423-426, 1983b

Garrot RA, Eberhardt LE, Hanson WC: Arctic fox denning behaviour in northern Alaska. Canadian Journal of Zoology 62: 1636-1640, 1984

Geffen E, Gompper ME, Gittleman JL, Luh HK, Macdonald DW, Wayne RK: Size, life-history traits, and social organization in the Canidae: a re-evaluation. American Naturalist 147: 140-160, 1996

Goltsman M, Kruchenkova EP, Sergeev S, Johnson PJ, Macdonald DW: Effects of food availability on dispersal and sex ratio in the Mednyi Arctic fox. Behaviour, Ecology and Sociobiology 59: 198-206, 2005

Grandin T, Deesing MJ: Genetics and the behaviour of domestic animals. In: Behavioural Genetics and Animal Science. Academic Press, San Diego CA, ISBN no 0-12295130-1 (Chapter 1), 1998

Haapanen K, Harri M, Mononen J, Korhonen H, Niemelä P, Rouvinen K, Fors F: Lymodellens och andra miljöfaktorers inverka på blårävens valpresultat. In: NJF-Utredning/rapport nr. 60. Resultater af de seneste års nordisk pelsdyrforskning. Seminar nr. 185, September 19-21, Tåstrup, Denmark. Nordiske Jordbrugsforskeres Förening, 1990

Harri M, Ahola L, Kasanen S, Mononen J, Rekilä T: Housing design for farmed foxes based on key features of the environment. In: Frontiers in Laboratory Animal Science, p 136, Joint Conference of ICLAS, Scand-LAS and FinLAS, 2-6 July 1995, Helsinki, Finland. 1995

Harri M, Ahola L, Mononen J, Rekilä T: Attempts to improve the husbandry of farmed foxes. In: Modern concepts in evolutionary genetics. Proceedings of the Scientific Conference dedicated to Professor Dmitri K. Belayev, pp 369-371, 9-12 September, Novosibirsk, Russia. 1997

Harri M, Mononen J, Rekilä T, Ahola L, Pyykönen T: Attempts to improve reproductive performance of farmed foxes. In Tyutyunnik NN, Ilukha VA, Kozhevnikova, Oleinik VM (eds.): II International Symposium, Physiological bases for increasing the productivity of predatory fur animals, 15-17 September, Petrozavodsk, Russia. 1998a

Harri M, Mononen J, Rekilä T, Korhonen H, Niemelä P: Effects of top nest box on growth, fur-quality and behaviour of blue foxes during their growing season. Acta Agriculturae Scandinavica Section A Animal Science 48: 184-191, 1998b

Harri M, Mononen J, Rekilä T, Rouvinen K: Comparison of two breeding systems for timing of whelpings in farmed silver foxes. Agricultural and Food Science in Finland 8: 3-8, 1999

Harri M, Karhunen H, Mononen J, Kasanen S: Stress-induced responses in farmed blue foxes. Scientifur 24 (IV-b: Behaviour and welfare), 118-120, 2000

Harri M, Mononen J, Ahola L, Plyusnina I, Rekilä T: Behavioural and physiological differences between silver foxes selected and not selected for domestic behaviour. Animal Welfare 12: 305-314, 2003

Hart BL: The behaviour of domestic animals. pp 1-260, W.F. Freeman and Company. New York. USA, 1985

Hemsworth PH, Barnett JL, Hansen C, Gonoyou HW: Te influence of early contacts with humans on subsequent behavioural response of pigs to humans. Applied Animal Behaviour Science 15: 55-63, 1986

Hemsworth PH, Coleman GJ, Barnett JL, Borg S, Dowling S: The effects of cognitive behavioral intervention on the attitude and behavior of stockpersons and the behavior and productivity of commercial dairy cows. Journal of Animal Science 80: 68-78, 2002.

Henderson CR: Best linear unbiased estimation and prediction under a selection model. Biometrics 31: 423–447, 1975

Hernesniemi T, Knutar TA: Kettujen hoito eri tuotantokausina (Management in fox breeding in different production stages) In: Hernesniemi T (Ed.): Ketunkasvatuksen taito. pp 68-105, Opetushallitus, Jyväskylä, Finland, 2000

Hersteinsson P: The behavioural ecology of the arctic fox (*Alopex lagopus*) in Iceland. Doctoral thesis, University of Oxford, 1984

Hersteinsson P, Macdonald DW: Some comparisons between red and arctic foxes, *Vulpes vulpes* and *Alopex lagopus* as revealed by radio-tracking. Symposia of the Zoological Society of London 49: 259-289, 1982

Hersteinsson P, Macdonald DW: Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos 64: 505-515, 1992

Hersteinsson P, Macdonald DW: Diet of arctic foxes (*Alopex lagopus*) in Iceland. Journal of Zoology (London) 240: 457-474, 1996

Hiruki LM, Stirling I: Population dynamics of the arctic fox, *Alopex lagopus* on Banks Island, Northwest territories. Canadian Field Naturalist 103: 380-387, 1989

Hrdy SB: Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology 1: 13-40, 1979

Ilukha V, Harri M, Rekilä T: Reproductive success of farmed blue foxes. Journal of Animal Breeding and Genetics 114: 465-474, 1997

Ilukha V, Mononen J, Pyykönen T, Nurminen L, Harri M: Survival and growth of blue fox cubs from small and large litters. In: Miettinen, M. (Ed): NJF report, NJF-seminar 347, 2-4 October 2002, Vuokatti, Finland, 2002

Ilukha V, Rekilä T, Pyykönen T, Mononen J: Maternal infanticide is more common in farmed silver foxes (*Vulpes vulpes*) than blue foxes (*Alopex lagopus*) In: Hänninen L, Valros A (Eds): Proceedings of the 38th International Congress of the ISAE. p 159, 3-7 August 2004, Helsinki, Finland. 2004

Jalkanen L: Sperm quality in silver fox, variation and relation to the breeding results. In: Tauson AL, Valtonen M (Eds.): Reproduction in carnivorous fur bearing animals. Nordic Association of Agricultural Scientists, Report no. 75, pp 139-143, Copenhagen, Denmark, 1992

Jalkanen L, Joutsenlahti U: Present and future use of artificial insemination in fox breeding in Finland In: Murphy BD, Hunter DB (Eds.): Biology, Pathology and genetics of fur bearing animals. Proceedings of IV International Congress in Fur Animal Breeding, August 21-24, 1988. University of Saskatchewan Press, Saskatchewan, Canada. 1988

Jeppesen LL, Pedersen V: Improvement of management routines and cage systems in fox production. Scientifur 14: 237-242, 1990

Jezierski T, Jaworski Z, Górecka A: Effects of handling on behaviour and heart rate in Konik Horses: comparison of stable and forest reared young stock. Applied Animal Behaviour Science 62: 1-11, 1999

Kennedy AJ: Site variation in summer foods of arctic fox, Prince of Wales Island, Northwest Territories. Arctic 33: 366-368, 1980

Kenttämies H, Smeds K: Genetic change in confidence and some production traits in blue foxes (*Alopex lagopus*) selected for confident behaviour. Proceedings of the VII International Scientific Congress in Fur Animal Production. Kastoria 2000. Scientifur Vol III-B Genetics 24: 107-109, 2000

Kenttämies H, Valberg Nordrum N, Brenœ UT, Smeds K, Johannessen KR, Bakken M: Selection for more confident foxes in Finland and Norway: Heritability and selection response for confident behaviour in blue foxes (*Alopex lagopus*). Applied Animal Behaviour Science 78: 67-82, 2002

Korhonen H, Niemelä P: Evaluation of the relationship between social status and reproductive performance in farmed blue foxes. Reproduction, Nutrition, Development 33: 289-295, 1993

Korhonen H, Alasuutari S: Social relationships and reproductive performance in group-living arctic blue foxes. Agricultural Science in Finland 3: 351-361, 1994

Korhonen HT, Alasuutari S: Dominance relations in captive groups of adult and juvenile arctic blue foxes (*Alopex lagopus*). Polar biology 15: 353-358, 1995

Korhonen HT, Niemelä P: Comparison of production results between blue foxes housed with and without platforms. Agricultural Science in Finland 4: 351-361, 1995

Korhonen H, Niemelä P: Effect of environmental and social enrichment on some welfare variables in farm blue foxes (*Alopex lagopus*). Scientifur 20: 26-34, 1996a

Korhonen H, Niemelä P: Temperament and reproductive success in farm bred silver foxes housed with and without platforms. Journal of Animal Breeding and Genetics 113: 209-218, 1996b

Korhonen HT, Niemelä P: Enrichment value of wooden blocks for farmed blue foxes (*Alopex lagopus*). Animal Welfare 9: 177-191, 2000

Korhonen HT, Alasuutari S, Mäkinen A, Niemelä P: Inter- and intraspecific competition between the fox species *Alopex lagopus* and *Vulpes vulpes*: an evaluation trial under penned conditions. Polar biology 17: 330-336, 1997

Korhonen HT, Rekilä T, Jauhiainen L: Effects of year-round nestbox and temperament on welfare in blue foxes. International Congress of the International Society for Applied Ethology 40, Annals of animal science 6: 149-167, 2006

Koskinen N, Sepponen J, Kupsala K, Rekilä T: Effects of early selection and body conditioning of young blue fox, *Alopex lagopus*, females on breeding result, a field study. Proceedings from the NJF-Seminar No 403, 13-15 August, Kolding. Denmark. Nordic Association of Agricultural Scientists, 2007

Kullberg C, Angerbjörn A: Social behaviour and cooperate breeding in arctic foxes, *Alopex lagopus* (L.), in a semi-natural environment. Ethology 90: 321-335, 1992

Ladevig J: Development of the concept of stress and its application to farm animal behaviour research In: Appleby MC, Horrell RI, Petherick JC, Rutter SM (Eds.). Society for Veterinary Ethology, 5th Anniversary 1966-1991. Applied animal behaviour: past, present and future. Proceedings of the International congress, pp 114-117. Universities Federation for Animal Welfare, Potters Bar, Edingburgh, UK. 1991

Lawrens E (Ed): Henderson's dictionary of biological terms. 11th edition. Longman Group Limited, 1995

Lindström E: Territory inheritance and the evolution of group-living in carnivores. Animal Behaviour 34: 1825-1835, 1986

Lund V: Ethics and animal welfare in organic animal husbandry. Doctoral dissertation. Deptartment of Animal Environment and Health, SLU. Acta Universitatis Agriculturae Suecidae vol. 137, 2002

Maa- ja metsätalousministeriön päätös turkiseläinten pidolle asetettavista eläinsuojeluvaatimuksista (16/EEO/1999). Ministry of Agriculture and Forestry decree on animal welfare requirements, 1999

Macdonald DW: Social factors affecting reproduction amongst red foxes (*Vulpes vulpes L.*). Biogeographica 18: 123-175, 1980

MacEwen EH, Scott A: Pigmented areas in the uterus of the arctic fox *Alopex lagopus* innuituis Merriam. Proceedings of the Zoological Society of London 128: 3487-379, 1957

MacPherson AH: The dynamics of Canadian arctic fox populations. Canadian Wildlife Service Report Series 8: 1-52, 1969

Malm K: Behaviour of parents and offspring in two canids. Swedish University of agricultural Sciences, Faculty of Veterinary Medicine. Report 37, 87 pp, Skara, Sweden, 1995

Manocha S: Abortion and cannibalism in squirrel monkeys (*Saimiri sciureus*) associated with experimental protein deficiency during gestation. Laboratory Animal Science 26: 649-650, 1976

Martin P, Bateson P: Measuring behaviour: An introductory guide, pp 84-100, 2nd edition, Cambridge University Press, Cambridge, Great Britain, 1993

Mateo JM, Aitken DH, Bodnoff S, Sapolsky RM: Effects of differential handling on the behaviour of domestic ewes (*Ovis aries*). Applied Animal Behaviour Science 32: 45-54, 1991

Millar JS: Adaptive features of mammalian reproductive optima. Oikos 45: 290-292, 1977.

Moberg GP: How behavioural stress disrupts the endocrine control of reproduction in domestic animals. Journal of Dairy Sciences 74: 304-311, 1991

Moberg GP: Biological response to stress: implications for animal welfare. In: Moberg GP and Mench JA (Eds). The Biology of animal Stress, pp 1-21, CABI Publishing, CAB International, Wallingford, Oxon OX10 8DE, UK, 2000

Moehlman PD: Intraspecific variation in canid social systems. In: Gittleman JL (Ed.): Carnivore Behavior, Ecology, and Evolution, pp 143-163, Cornell University Press, Ithaca, New York, USA, 1989

Moe R: Investigation of methods to assess stress in farmed silver foxes (*Vulpes vulpes*). Ph.D. thesis, Norweigian College of Veterinary Medicine. Oslo, 1996

Mononen J, Harri M: Lentomelun vaikutus tarhaturkiseläimiin (The effect of aviation noise on farmed fur animals). Turkistalous 3-4: 60-62, 1991

Mononen J, Harri M, Sepponen J, Korhonen H, Rekilä T, Ahola L: A top and a floor box as breeding nest boxes in farmed blue foxes (*Alopex lagopus*): reproductive performance, use of boxes and cub carrying. Acta Agricultural Scandinavica Section A Animal Science 49: 206-210, 1999

Mononen J, Pulkkinen H, Pyykönen T, Juntunen J, Hänninen S, Ahola L: Lentomelun vaikutus tarhattujen sinikettujen lisääntymiseen: esitutkimus (The effects of aviation noise on reproduction in farmed blue foxes: a pilot study). Suomen eläinlääkärilehti 109: 337-343, 2003

Moss S, Östberg G: Lyförsök med blåräv 1984. Finsk Pälstidskrift 19: 120-121, 1985

Møller OM, Mondain-Monval M, Smith A, Metzger E, Scholler R: Temporal relationships between hormonal concentrations and the electrical resistance of the vaginal tract of blue foxes (*Alopex lagopus*) at pro-oestrus and oestrus. Journal of Reproduction and Fertility 70: 15-24, 1984

Nara BS, First NL: Effect of indomethacin and prostaglandin $F_2\alpha$ on parturition in swine. Journal of Animal Science 52: 1360-70, 1981

Nieminen P, Pyykönen T, Asikainen J, Mononen J, Mustonen AM: Effects of fasting and exogenous melatonin on annual rhythms in the blue fox (*Alopex lagopus*). Comparative Biochemistry and Physiology A 139: 183-197, 2004

Nikula S: Temperament of foxes at private farms: Heritability and association with reproduction traits. In: Proceedings from the NJF-Seminar No 280, Report no. 116, pp 219-226, 8-10 October, 1997, Helsinki, Finland. Nordic Association of Agricultural Scientists, 1997

Nikula S, Smeds K, Hietanen H, Kenttämies H, Ojala M: Confident behaviour and production traits – results from a field study of foxes. Proceedings of the VII International Scientific Congress in Fur Animal Production. Kastoria 2000. Scientifur Vol III-B Genetics 24: 99-102, 2000

Nimon AJ, Broom DM: The welfare of farmed foxes *Vulpes vulpes* and *Alopex lagopus* in relation to housing and management: a review. Animal Welfare 10: 223-248, 2001

Nordrum NV, Brenœ, Johannessen KR, Bakken M: Selection for increased confidence in foxes, and possible consequences fro production economy. Proceedings of the VII International Scientific Congress in Fur Animal Production. Kastoria 2000. Scientifur Vol III-B Genetics 24: 98, 2000

Norodd Nes N, Einarsson EJ, Lohi O: Beautiful fur animals and their colour genetics, pp 90-91, Scientifur, Glostrup, Denmark, 1988

Osadchuk LV, Braastad BO, Hovland AL, Bakken M: Handling during pregnancy in the blue fox (*Alopex lagopus*): The influence on the fetal pituitary-adrenal axis. General and Comparative Endocrinology 123: 100-110, 2001

Osadchuk LV, Braastad BO, Hovland AL, Bakken M: Handling during pregnancy in the blue fox (*Alopex lagopus*): the influence on the fetal gonadal function. Endocrinology 132: 190-197, 2003a

Osadchuk LV, Braastad BO, Hovland AL, Bakken M: Reproductive and pituitary-adrenal axis parameters in normal and prenatally stressed prepubertal blue foxes (*Alopex lagopus*). Animal Science 76: 413-420, 2003b

Pedersen V: Early experience with the farm environment and later effects on behaviour in silver and blue foxes. Behavioural Processes 25: 163-169, 1991

Pedersen V: Handling of silver foxes at different ages pre-weaning and post-weaning and effects on later behaviour and stress-sensitivity. Norwegian Journal of Agricultural Science 9: 529-535, 1992

Pedersen V: Early experience in silver foxes and effects on later behavioural and physiological parameters. Ph.D. thesis, University of Copenhagen, Denmark, 1993a

Pedersen V: Effects of different post-weaning handling procedures on the later behaviour of silver foxes. Applied Animal Behaviour Science 37: 239-250, 1993b

Pedersen V: Long-term effects of different handling procedures on behavioural, physiological, and production-related parameters in silver foxes. Applied Animal Behaviour Science 40: 285-296, 1994

Pedersen V: Parvis eller solitær opvækst: Effekt på adfærd, vægtudvikling ogreproduction hos blåræve. Pelsdyrerhvervets Forsøgs- & Rådgivningsvirksomhet A/S, Faglig Årsberetning, 1997

Pedersen V, Jeppesen LL: Effect of early handling on later behaviour and stress responses in the silver fox (*Vulpes Vulpes*). Applied Animal Behaviour Science 26: 383-393, 1990

Pedersen V, Jeppesen LL: Daytime use of various types of whole-year shelters in farmed silver foxes *Vulpes vulpes* and blue foxes *Alopex lagopus*. Applied Animal Behaviour Science 36: 259-273, 1993

Pedersen V, Moeller NH, Jeppesen LL: Behavioural and physiological effects of post-weaning handling and access to shelters in farmed blue foxes (*Alopex lagopus*). Applied Aimal Behaviour Science 77: 139-154, 2002

Peura J, Strandén I: Siniketun kokoa jalostetaan hedelmällisyyden kustannuksella. Turkistalous 8-9: 13-15, 2003

Peura J, Strandén I, Smeds K: Genetics of litter size, age at first insemination and animal size in blue fox (*Alopoex lagopus*). In Urlings B, Spruijt M, Ruis L, Boekhorst (Eds.): Proceedings of the VIII International Scientific Congress in Fur Animal Production, 15-18 September 2004, 'S-Hertogenbosch, the Netherlands, Part IV-3RP. Scientifur, 28: 206-210, 2004a

Peura J, Serenius T, Strandén I: Economic weights for litter size and skin character traits in Finnish blue fox production. In: Proceedings from the XXI Genetic Days, 1-3 September 2004, Wroclaw, Poland. Animal science papers and reports 22, 2: 81-86, 2004b

Prestrud P: Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. Arctic 44: 132-138, 1991

Prestrud P: Food habits and observations of the hunting behaviour of arctic foxes, *Alopex lagopus*, in Svalbard. Canadian Field Naturalist 106: 225-236, 1992a

Prestrud P: Physical characteristics of arctic fox (*Alopex lagopus*) dens in Svalbard. Arctic 45: 154-158, 1992b

Prestrud P: Denning and home range characteristics of breeding arctic foxes in Svalbard. Canadian Journal of Zoology 70: 1276-1283, 1992c

Price EO: Behavioural development in animals undergoing domestication. Applied Animal Behaviour Science 65: 245-271, 1999

Pylkkö P, Korhonen H, Sepponen J, Rekilä T, Lindeberg H: Siniketlujen lisääntymisprojektin tuloksia. In: Leena Jokela (Ed.) Rehunvalmistajien luentopäivät, 15-16 February, Jyväskylä, Finland. 2005

Pyykönen T, Ahola L, Jalkanen L, Harri M: Behaviour of silver foxes (*Vulpes vulpes*) in ground floor enclosures. In: Proceedings of the NJF-seminar no 116, pp 125-131, 6-8 October 1997, Helsinki, Finland. 1997

Pyykönen T, Asikainen J, Miettinen M, Mononen J, Sepponen J, Ahola L: Breeding success of farmed silver foxes with top boxes. In: Miettinen M (Ed): Proceedings of the NJF-seminar no 347, subsection for fur animals, pp 127-132, 2-4 October, 2002, Vuokatti, Finland. 2002a

Pyykönen T, Ahola L, Mononen J, Mohaibes M, Kasanen S: Parental behaviour of group-housed farmed silver foxes in semi-natural environment. In: Koene P (Ed), the Scientific Committee of the 36th ISAE Congress. Proceedings of the 36th International Congress of the ISAE, p 214, 6-10 August 2002, Zuiderduin, the Netherlands. 2002b

Pyykönen T, Korhonen HT, Ahola L, Mohaibes M, Hänninen S, Sepponen J, Mononen J: Lower housing density combined with stable social environment improves reproductive performance of primiparous silver fox vixens. VIII International Scientific Congress in Fur Animal Production, 15-18 September 2004, Netherlands. Scientifur 28: 38, 2004

Rekilä T: Behavioural tests in welfare research of foxes. Kuopio University Publications C. Natural and Environmental Sciences 92, 1999

Rekilä T, Harri M, Ahola L: Validation of the feeding test as an index of fear in farmed blue (*Alopex lagopus*) and silver foxes (*Vulpes vulpes*). Physiology and Behaviour 62: 805-810, 1997

Rekilä T, Harri M, Jalkanen L: Effect of enlarged breeding nest box on reproductive success on blue foxes (*Alopex lagopus*). In Tyutyunnik NN, Ilukha VA, Kozhevnikova, Oleinik VM (Eds.): II International Symposium, Physiological bases for increasing the productivity of predatory fur animals, p 118, 15-17 September 1998, Petrozavodsk, Russia. 1998

Rushen J: Problems associated with the interpretation of physiological data in the assessment of animal welfare. Applied Animal Behaviour Science 28: 381-386, 1991

Rushen J: Changing concepts of farm animal welfare: bringing the gap between applied and basic research. Applied Animal Behaviour Science 81: 199-214, 2003

Rushen J, Taylor AA, de Passillé AM: Domestic animals' fear of humans and its effect on their welfare. Applied Animal Behaviour Science 65: 285-303, 1999

Sanson GH, Farstad W: Perinatal pup loss in the blue fox (*Alopex lagopus*) review and historical data. In: Proceedings from NJF-Seminar, No. 354, 8-10 October 2003, Lillehammer, Norway. 2003

Sklepkovych BO: Kannibalism hos fjällrävar, *Alopex lagopus*, I de svenska lapplandsfjällen. Fauna och flora 84: 145-150, 1989

Smeds K: Rävens fruktsamhetsegenskapers arvbarhet. (The heritability of reproductive capacity of farmed foxes) Kotieläinjalostuksen tiedote No 95. Kotieläinten jalostustieteen laitos, University of Helsinki, University Press. 1992

Stearn J and Levine S: Pituitary-adrenal activity in the postpartum rat in the absence of suckling stimulation. Hormones and Behaviour 3: 237-246, 1972

Stearns SC and Hoekstra RF: Evolution an introduction. Oxford University Press Inc., New York. 2000

Stickney A: Seasonal patterns of prey availability and the foraging behaviour of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Canadian Journal of Zoology 69: 2853-2859, 1991

Strand O, Linnell JDC, Krogstad S, Landa A: Dietary and reproductive responses on arctic foxes to changes in small rodent abundance. Arctic 52: 272-278, 1999

Strand O, Landa A, Linnell J DC, Zimmermann B, Skogland T: Social organization and parental behaviour in the arctic fox. Journal of Mammalogy 81: 223-233, 2000

Stranden I, Peura J: Ketuille uusi hedelmällisyyden indeksilaskenta. Turkistalous 10: 11-13, 2004

Szor G, Berteaux D, Gauthier G: Finding the right home: distribution of food resources and terrain characteristics influence selection of denning sites and reproductive dens in arctic foxes. Polar Biology 31: 351-362, 2008

Tannerfeldt M, Angerbjörn A: Life history strategies in a fluctuating environment: establishment and reproductive success in the arctic fox. Ecography 19: 209-220, 1996

Tannerfeldt M, Angerbjörn A: Fluctuating resources and the evolution of litter size in the arctic fox. Oikos 83: 545-559, 1998

Trut L: Early Canid Domestication: The Farm-fox Experiment. American Scientist 87:160-169, 1999

Tuljapurkar SD: Population dynamics in variable environments. IV. Cyclical environments, sensitivity analysis and dynamics. Theoretical Population Biology 28: 1-17, 1985

Valberg Nordrum NM: Genetic and phenotypic parameters of litter size traits in the blue fox (*Alopex lagopus*). Acta Agriculturae Scandinavica Section A Animal Science 46: 61-64, 1996

Valtonen M, King WA, Gustavsson I, Mäkinen A: Embryonic development in the blue fox. Nordisk Veterinaermedicin 37: 243-248, 1985

Waiblinger S, Boivin X, Pedersen V, Tosi MV, Janczac AM, Visser EK, Jones RB: Assessing the human-animal relationship in farmed species: A critical review. Applied Animal Behaviour Science 101: 185-242, 2006

Wright JC: The effects of differential rearing on exploratory behaviour in puppies. Applied Animal Ethology 10: 27-34, 1983

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