THE WELFARE OF FARMED FOXES *VULPES VULPES* AND *ALOPEX LAGOPUS* IN RELATION TO HOUSING AND MANAGEMENT: A REVIEW

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Abstract

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Foxes have been kept in captivity in Europe for the purpose of fur production for 70–80 years. In comparison with the main domesticated animal species, this is a very recent intervention. This paper reviews available evidence concerning the welfare of farmed foxes in relation to housing and management. The bulk of the literature relates to early handling of cubs, with the intention of reducing their subsequent fear of humans, and to simple changes in the cage environment that may provide environmental enrichment for foxes. Fear of humans appears to be a significant and pervasive problem, and the barrenness of cages is also a cause for concern. The extent of abnormal behaviours and reproductive failure, both indicative of quite severe welfare problems, is not sufficiently documented. Some housing and management practices are less detrimental than others; nonetheless, the evidence suggests that the welfare of farmed foxes is poor.

Keywords: animal welfare, enrichment, fear, foxes, housing, management, reproduction

Introduction

There are two fox species involved in fur production on farms: the silver fox, a colour variety of the common red fox (Vulpes vulpes), and the blue fox, a variety of the Arctic fox (Alopex lagopus) (Burton 1979; Bakken et al 1994). The first silver foxes and blue foxes were kept on farms 80 and 70 years ago, respectively, but they have been kept in large numbers on fur farms for approximately 50 years. Thus, the question of whether or not they could be said to be domesticated arises, and this is relevant to the likelihood of good welfare under farm conditions. In comparison with species such as sheep, cattle, horses, dogs or llamas, which have been kept in captivity for more than 5000 years (Hemmer 1983), foxes have had only very recent contact with humans. Chromosome mapping of dogs and red foxes shows that they have many similarities but that the red fox is more similar to the ancestral carnivore type and that the dog or wolf karyotype has changed in many ways because of chromosomal fusion and fission events (Yang et al 1999). Almost all farmed foxes live in wire cages with very limited human contact. As Price (1997) has emphasised, domestication implies adaptation by genetic change occurring over generations, in addition to environmentally induced changes during the development of individuals, so the foxes have had little opportunity to become domesticated. The high level of adaptation reached by the main domestic animal species, which are relatively few in number, is suggested by the observation

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that the vast majority of individuals have the ability to breed with no problems, and most can tolerate some physical contact and prolonged human close proximity with no substantial physiological or behavioural responses. The domestic animals still have a full range of needs, including those to show certain behaviours (Broom & Johnson 1993), but these can be satisfied in appropriately designed captive environments and with appropriate management. The extent to which fear can be reduced by experience of human contact is reviewed in this paper, but the question remains: have foxes the capacity to adapt fully to farm conditions and, hence, can their welfare be good on farms?

This paper reviews available evidence concerning the welfare of farmed foxes in relation to housing and management. To supply some background information, we begin with an overview of housing conditions on farms and the biology of foxes in the wild. A more general, earlier review (Bakken *et al* 1994) concluded that the major welfare problems on fox fur farms are: a widespread and apparently considerable fear of humans; the barrenness of cages; and difficulties in reproduction. Bakken *et al* (1994) conceded that public criticism of these aspects of fox farms was entirely justified. The greater part of this review, therefore, focuses on evidence related to these issues.

The welfare of fur animals is the subject of some recommendations and codes of practice produced by government agencies or by the industry. The most comprehensive of these publications is the 'Recommendation Concerning Fur Animals', produced in 1999 by the Council of Europe Standing Committee of the European Convention for the Protection of Animals Kept for Farming Purposes. However, as these are not scientific publications, they are not discussed in this review.

The conditions on fur farms

Bakken *et al* (1994) described the standard conditions on fur farms. Foxes are kept in wire mesh cages with a floor area of $0.6-0.8 \text{ m}^2$, occasionally as much as 1.2 m^2 , and a height of 0.6-0.8 m, occasionally as much as 1.0 m. The smaller cage size is normally used for the blue fox. Cages are furnished with a nest box from the onset of the mating season until the weaning of the cubs. On most farms, for the rest of the year the foxes have nowhere to hide; a wire mesh platform is provided in some countries, and sometimes wooden platforms with or without solid sides are used.

Following birth, the vixen and her cubs are generally separated at eight weeks of age, and the cubs may be kept with littermates until 10 weeks of age. Pedersen (1991, 1992) reported that while the litter remained together, they were housed in double standard fox cages, measuring $1.95 \times 1.2 \times 0.95$ m. Thereafter, foxes may be kept singly or placed in male/female pairs (generally siblings) in either single or double standard cages (Pedersen & Jeppesen 1990; Pedersen 1991). Silver foxes are said to wean an average of two to four cubs per mated vixen, while blue foxes produce twice as many (Bakken *et al* 1994).

Farmed foxes are fed daily with nutritious minced or puréed food. They are caught and handled when measuring oestrus and during mating, fur grading, and medical treatment. On average, breeding animals are caught or moved up to 20 times per year, and cubs may be moved up to five times. Handling by humans and enclosure in a new cage are regular experiences.

Pelting occurs in November and December. Foxes, whether they are kept for pelting or breeding, are housed in cages in sheds. The cages are usually in rows with mutual walls but may be free-standing individual cages. The present farm environment developed from large ground enclosures holding many foxes, but in which hygiene was sometimes poor.

The biology of the red fox

The red fox is found throughout Europe and the Holarctic region, in barren tundra up to 75° N in Canada, and in the deserts of Australia — areas with no greater than 8 mm rain per year (Lloyd 1980a; Burton 1979). This enormous range is evidence of its adaptability, which in turn indicates a high capacity for learning. Correspondingly, the fox has been reported to have a "strong tendency to investigate the unfamiliar" (Lloyd 1980a, p 12).

A male fox reaches a maximum height of 35–40 cm tall at the shoulder (Burton 1979), with a head and body length of 56–77 cm and a tail length of 32–48 cm (Lloyd 1980b; see also Burton 1979). Male foxes generally weigh 6–10 kg, with a maximum of 14.3 kg recorded in Norway (Burton 1979). Vixens are usually a few centimetres shorter, and weigh on average a kilogramme less, although geographical variations exist and females in one region may be larger than males in another. Local geographical variations in body size may be related to population density (Cavallini 1995).

Habitat and home range

In whatever habitat a red fox occupies, cover is important (Lloyd 1980a). In open country, foxes may habitually live below ground (Burton 1979). Surface cover, such as cairns of rocks, boulders and undergrowth, are used as resting places, and foxes may sleep underground during bad weather (Burton 1979; Lloyd 1980a).

Many foxes become resident in a particular area and establish home ranges, the sizes of which vary considerably. Studies in Northern Ireland, Denmark, Holland and Switzerland show that estimated ranges of adult foxes vary from about 400 to 1600 ha each (Lloyd 1980b). In Oxfordshire (UK), where the terrain is a mixture of large gardens and farmland, home range sizes vary between 10 and 70 ha (Macdonald 1987); in nearby mixed farmland, they vary between 100 and 250 ha and, in the Arctic, they may be as large as 3000 ha. The dispersion of both appropriate resting shelters and available food strongly affects home range size (Lucherini *et al* 1995; Lucherini & Lovari 1996).

All areas of a home range are not used equally by foxes (Burton 1979; Lloyd 1980a); instead, researchers often detect areas of high use, and a series of pathways interconnecting these (eg Storm 1965; Maurel 1979). The occupation of different preferred zones within a home range tends to change over time (Ables 1969) and it has been noted, via observations in snow, that some regularly travelled paths are frequently urine-marked in the same places, whereas others are not urine-marked at all (Lloyd 1980b). The systematic activities of foxes within ranges has led some researchers to propose that foxes learn aspects of the spatial relations between places and hence obtain a form of cognitive map (Fabrigoule & Maurel 1982).

Social grouping and reproductive activity

Some foxes are solitary whereas others live in territorial pairs (eg Sargeant 1972) that may stay together as long as both animals live (Lloyd 1980a). Foxes may also live in small groups (Ables 1969; Macdonald 1980; Cavallini 1996) of various structures, often one adult male and three to four adult vixens that are closely related (such as a mother and her daughters). Evidence has accumulated that generally only one vixen within a social grouping will rear offspring. In Macdonald's (1979) study, this was always the most dominant female, although the dominant individual changed occasionally between years. The subordinate, non-breeding vixens may help to rear the cubs of the dominant female: they groom, guard and bring food to

the cubs. Within such groups, status-linked reproductive suppression occurs (Macdonald 1980).

The male fox may play an important role in rearing the cubs. Burton (1979) noted that there are many records of males being found with the vixen and her cubs, and described video footage of the family unit playing together. Macdonald (1979) also observed the males in his family groups feeding and playing with the cubs.

Birth and cub development

The vixen finds a dry, protected area in which to give birth, such as an earth den. Once cubs are born, she may move them from one earth to another (Lloyd 1980b; Burton 1979). The usual litter size is four to six cubs (Lloyd 1980b; Burton 1979; Macdonald 1987). Hypothermia of young cubs can be a problem (Braastad 1996) and vixens normally spend much time close to the earth during the first 7–10 days after parturition (Macdonald 1980).

At about six weeks of age the cubs begin to emerge from their earth, but do not venture further than a few metres from the den. Nutritional weaning is complete at eight weeks. In areas of abundant cover, the den is abandoned when the cubs are about 10 weeks old (Burton 1979). Cubs usually stay with the mother until they reach adult size at 6–7 months of age (Lloyd 1980a).

From approximately six months of age onwards, all male cubs and some female cubs will disperse from their natal territory (Hough 1979; Lloyd 1980a; Macdonald 1987), although some females will choose to stay (Macdonald 1980). Those that disperse may travel short distances (eg 2 km), but distances recorded include 52 km in Wales, 500 km in Sweden and 394 km in the USA (Lloyd 1980b; Macdonald 1987).

Social behaviour and sensory biology

Foxes have a sophisticated and intricate repertoire of social behaviour. A wide variety of play behaviours and sequences has been described (Burton 1979, p 40), and facial expressions accompanied by postures are used to convey information such as status (Macdonald 1987). Burton (1979) identified 28 individual calls, and recent sonographic analysis of vocalisations from 512 adults and 73 cubs suggested 20 call types, used both singly and in combination (Newton-Fisher *et al* 1993).

Foxes may be active by day, particularly where undisturbed by people (Burton 1979). Nonetheless, most activity occurs at dusk or nocturnally (Maurel 1979; Lloyd 1980b). Experiments with captive foxes suggest that foxes are likely to rely on hearing at night, their ears being sensitive to low-pitched sounds such as the rustling of a vole in the grass (Burton 1979). The range and complexity of fox vocalisations also testifies to the importance of the foxes' auditory environment.

As with mink (Nimon & Broom 1999), olfactory variables play an important role in the lives of wild foxes. Foxes scent-mark extensively, having several scent glands — a tail gland, two anal sacs and glands in the skin between their toes and pads. Although little is known about the function of the secretion from the latter, Macdonald (1987) noted that a bloodhound (and thus presumably another fox) could follow the scent for about 20 minutes after the animal had passed. Foxes sprinkle urine on empty cache sites, apparently as a reminder not to explore these again later, and Macdonald (1987) states that "fox urine is clearly an important feature of the vulpine lifestyle. Expression of social superiority in face-to-face encounters may be one function of scent" (p 124). Furthermore, he added that the insulating properties of grass, woodlands and open plough, together with the effects of wind and shade, must make each fox's territory an ever-shifting patchwork of olfactory

information. He suggested, for example, that trespassing foxes may chart a route through poorly scented terrain. This is an aspect of their environment that we cannot sense.

The biology of the Arctic fox

Burton (1979) remarked that, apart from the polar bear, no other carnivore is virtually confined to the tundra, nor so well adapted to life in cold climates. Arctic foxes are smaller than red foxes: in males, the height at the shoulder is 30 cm, the body length is 50–65 cm, the tail extends 28–33 cm, and weight ranges from 4.5 to 8 kg.

On the tundra, they do not hibernate but remain active and have been seen hunting in temperatures of -45° C (Burton 1979). Unlike the red fox, the Arctic fox is nomadic. It can travel many kilometres off shore over pack ice. Perry (1973) recorded a marked fox travelling 9000 km from its birthplace. The Arctic fox has been described as less wary of humans than the red fox, and often enters the camps of visitors to the Arctic to be hand-fed (Burton 1979).

In most other aspects of biology and behaviour, the Arctic fox is very similar to the red fox. Macdonald (1987) considered that red foxes probably treat Arctic foxes as inferior conspecifics and Frafjord *et al* (1989) describe their interactions. Where fur harvesters have introduced them to the same island, it is clear that the red fox out-competes the Arctic fox (Macdonald 1987).

Summary of biology and relationship to fur farms

Extensive studies of these foxes throughout their distribution have revealed that they are complex animals. They spend a long time rearing their cubs. Many individuals that have been monitored travel long distances, and red foxes make patterned use of large home ranges. Social behaviour is varied, and social status is evidently important, strongly affecting group relations and productivity. Males, as well as non-breeding vixens, play a role in rearing the cubs. Reproduction is evidently controlled by complex factors, including social interaction, and can vary considerably across years and locations. Foxes seek cover regularly, and make use of several dens. Those wary of conspecifics may attempt to avoid leaving scent trails, and the relative importance of scent-marking of paths and caches via urine or gland secretions has not been fully assessed. Foxes are probably capable of a high degree of learning, including the possible use of cognitive maps.

The red fox has been described as the most successful European carnivore because it has survived persecution and even flourished during the spread of urban development (Burton 1979). However, although urban development does not necessarily deprive foxes of their needs, it is clear that the barren, socially artificial conditions on fur farms are likely to do so.

Excessive fear of humans: modification by selective breeding

Farmed foxes are reported to exhibit "extreme fear" involving trembling, defecating, withdrawing to the back of the cage, and attempting to bite handlers (Tennessen 1988, p 392). Bakken *et al* (1994) referred to a state of "continuous" fear. These responses were found by Moe and Bakken (1998) to be comparable to human fear responses and were associated with stress-induced hyperthermia.

In a large-scale domestication experiment in Siberia, silver foxes were selectively bred for the elimination of negative, defensive responses to humans (Belyaev & Trut 1963; Belyaev 1979). This produced a population of foxes that behaved rather like domestic dogs; see

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photographs in Trut (1995). In a two-year study comparing 150 cubs from the selected population with 123 cubs from unselected foxes bred for commercial purposes, Belyaev et al (1985) found that domestication extended the period during which cubs could habituate to people. Cubs from the selected population showed enhanced sensory development (eg accelerated eye opening) and the sensitive period for socialisation was prolonged to 65 days of age. They showed no fearful behaviour towards the novel stimulus of being placed in a new cage, and they exhibited less fear than controls in response to humans. The control cubs had a shorter socialisation period (lasting up to 45 days), following which they exhibited fear in response to novel stimuli. These studies suggest that selective breeding for domestication in silver foxes can significantly reduce fear responses not only to humans, but also to novel stimuli. It has also been reported that females from the selected fox population come on heat earlier, and that fertile mating sometimes occurs twice a year (Naumenko & Belyaey 1980; Trut 1981). Further experiments using fox populations selected for domesticated behaviour have suggested that changes in brain chemistry accompany the divergence between tame and wild foxes (Popova et al 1991; Dygalo & Kalinina 1994), and that domestication affects the development of the pituitary system, which is involved in the expression of fear and aggression in mammals (Malyshenko 1982; Trut & Oskina 1985; Plyusnina et al 1991).

Other tests of foxes selectively bred for lack of fear towards humans have recently produced similar results. Harri *et al* (1997) purchased, from Russia, silver foxes (strain A) that had been selectively bred in this way for 37 generations. After weaning, they were housed, one animal per standard wire mesh cage, either (A1) with strain A neighbours or (A2) with normal farm strain B neighbours. In adulthood, their behaviour was compared with that of nine strain B foxes. A higher proportion of both A1 and A2 foxes ate, despite a human standing in front of their cage, than did B foxes (P < 0.001). A higher proportion of these A foxes accepted a hand-fed treat than did B foxes (P < 0.001). In what is referred to as a 'pair contest situation' against B foxes, A foxes monopolised food in 9 out of 10 cases. The A foxes had lower concentrations of plasma cortisol before and 20 minutes after handling than did the B foxes. Differences between the A1 and A2 groups were not significant. Thus, it seems that selection for reduced fear over many generations caused foxes to show significantly reduced behavioural and physiological responses to people and handling, and may have improved confidence with regard to other foxes, despite the neighbours amongst which they were housed.

These results highlight the importance of work that examines the physiological and behavioural responses of selectively bred foxes to standard stimuli in the farm environment, at different ages and under the various conditions that occur frequently (eg regular rehousing). Bakken *et al* (1994) cited several shorter-lasting selection experiments in Nordic countries, which, they reported, also show that it is possible to select against fear and in favour of curiosity. Further selection programmes are in progress and papers reporting these are expected.

Excessive fear of humans: modification by early handling and regular contact

In an attempt to reduce fear of humans and the farm environment in general, researchers have examined the possibility of early handling and human contact as an effective treatment. Pedersen and Jeppesen (1990) reviewed a number of studies which showed that handling early in the life of captive or domestic animals is often associated with less fear, more exploratory behaviour, and a better ability to cope in novel situations. Their review suggested that the best results occur when animals are handled during their sensitive periods for socialisation, although positive results had been achieved when handling took place before or

afterwards. Separation from the mother occurs much earlier on farms than in the wild and the period immediately after separation is likely to be a period of sensitivity to human socialisation.

Elaborate handling procedures

Tennessen (1988) examined the effects of regular human contact on silver fox cubs. Three treatments were involved: five minutes of play with a handler each weekday (group 1); being picked up briefly each weekday (group 2); or no extra handling (group 3). Tests of fear and exploratory behaviour at 15 weeks and at 6 months showed that those in group 1 showed less fearful and more exploratory behaviour in a novel situation, and the group ranking of fearful behavioural responses to the presence of a human outside the cage was ordered 3 > 2 > 1. Pedersen and Jeppesen (1990) exposed 32 silver fox cubs to a handling treatment in which they were fondled and talked to in the cage for five minutes, twice a day, six days a week, from two to eight weeks of age (ie including the socialisation period). Control cubs (n = 46)were not exposed to handling during this time. The cubs were not differentially treated between eight and 12 weeks, and all were subjected to normal farm procedures. At the age of 12, 15, 18 and 20 weeks, all cubs were tested with three different behavioural tests, including close eye-contact with a human, a hand punched rapidly towards the cage without hitting it, and a glove on a stick pushed into the cage. At the age of 24 weeks, all foxes were bloodsampled and exposed to an open field test — a measure of fear and exploration in a new, larger cage arena. The results demonstrated that the group handled during early development showed a significantly reduced fear response in tests made at later ages. The effect seemed to be related to all humans, not only to those who performed the handling. The behavioural and physiological results from the open field test were interpreted as suggesting that the control group experienced chronic stress, whereas the handled group were thought to be generally less stressed by their farm environment.

In a large-scale study, Pedersen (1992) investigated the effects of early handling at different ages in 344 silver fox cubs. Seven groups were handled at different ages before, during and after weaning, for either three, six or 12 weeks. Handling occurred twice a day for five minutes, five days a week, and involved fondling and talking to the cub. Cubs were subjected to the behavioural tests of response to a human outside the cage, and response to a human opening the cage door and reaching out to the fox, at 18, 24, 30 and 32 weeks.

Results indicated that, in comparison with a control group, foxes handled during or after weaning for three weeks or more later showed reduced fear responses towards humans at all ages tested except for 30 weeks. Again, the changing of experimenters suggested that this effect generalised to all humans and not just those who had done the handling. Pedersen (1992) suggested that the failure to find a significantly lower fear response in handled cubs at 30 weeks of age was the effect of a single blood-sampling session at 26 weeks (thus causing a temporary association between appearance of a human and pain). Results also suggested that handling before weaning (at eight weeks of age) had to be performed for six weeks or more to produce a reduction in fearfulness. These results do not compare exactly to the suggestions arising from Belyaev *et al*'s (1985) discussion of socialisation periods: in Pedersen's study, handling was most effective when targeted at cubs of approximately 56 days of age, rather than the 35 to 45 day 'optimal' period suggested by the earlier work.

Forceful versus gentle handling

Pedersen (1993a) furthered the results of her earlier experiments with a study of silver fox cubs assigned to control, forceful handling or gentle handling, twice daily for three weeks

post-weaning. Forceful handling involved capturing the cub with one hand on its tail and one under its stomach, transporting it to a smaller cage for two minutes, then capturing it in the same manner and returning it to the home cage. During gentle handling, the human slowly opened the cage door, fondled the cub and offered scraps of food, making no fast movements and withdrawing if the cub showed signs of fear. Behavioural tests were again used to compare groups at 18, 24, 30 and 32 weeks of age, on this occasion involving responses to the same two tests as reported in Pedersen (1992), as well as the glove test reported in Pedersen and Jeppesen (1990).

Although both handled groups showed less fear and more exploratory behaviour than the control group, it was not possible to conclude that one handling technique was more beneficial than the other in habituating foxes to the farm environment and its associated disturbances. Gently handled foxes reacted to humans, both known and unknown to them, with fewer fear responses and less disturbance of normal behaviour, but forcibly handled foxes showed more exploratory behaviour when exposed to novel stimuli.

Pedersen (1994) then questioned whether these early handling treatments might have beneficial effects in the longer term also. She noted that many studies have found early handling of farm animals to have immediate or short-term benefits on behaviour or physiology (eg Hemsworth et al 1981; Hargreaves & Hutson 1990; Podberscek et al 1991), but sometimes also suggested that later benefits accrued (Heird et al 1986). Firstly, she reported that the female foxes used in Pedersen (1993a) were compared during their first breeding season and it was found that forcibly handled vixens showed better reproductive performance than both gently handled and non-handled vixens (Pedersen 1993b). Secondly, she tested the same subjects used in Pedersen (1993a) with the same tests at 10, 13, 15 and 18 months of age. The results indeed showed that handling of foxes for three weeks postweaning had long-lasting effects on both behavioural and physiological parameters, but little effect on production-related parameters. Both handled groups showed significantly reduced fear reactions to the tests in comparison with controls; however, the effects of 'forced' handling were more pervasive. Gently handled animals showed reduced fear when a human stood outside the cage and when a novel object was put in the cage, but only forcibly handled animals continued to show reduced fear in response to the cage door opening and the human reaching for the animal. Pedersen (1994) offered the explanation that the positive association developed during gentle handling, which was specifically associated with feeding, may have been overshadowed by experience of normal farm procedures, such as capture, heat determination, etc. Both handled groups had significantly lower adrenal mass at 22 months of age, suggesting generally lower stress levels. Parameters such as body weight, body size, gastric ulceration (the extent of which was low) and pelt quality were not significantly different between the three groups, thus early handling cannot be considered an economic risk. A further conclusion from this study was that non-handled foxes were chronically stressed, as indicated by their high adrenal mass and high levels of fear.

Clear effects of handling on reproduction and fear of humans were apparent in a study of 87 primiparous blue fox vixens by Dalsgaard and Pedersen (1999). Half of the vixens had been handled gently as cubs from seven to 10 weeks of age for two minutes per day, five days per week, whereas the other half were non-handled controls. Handled vixens came into heat earlier, weaned more cubs and showed reduced fear responses to some test situations.

Visual experience and handling

In an alternative approach, Pedersen (1991) exposed cubs to constant visual contact with the farm environment (rather than actual handling) from two to eight weeks of age. For cubs in

the experimental group (both silver fox cubs [n = 71] and blue fox cubs [n = 141]), the solid wooden walls of the usual nest box were removed to reveal mesh walls when cubs were two weeks of age. The control group (33 silver fox cubs and 77 blue fox cubs) were left with standard wooden nest boxes. Cubs were again weaned at eight weeks by removal of the vixen, and then at 10 weeks placed in new cages in pairs. Tests of behavioural response to a human outside the cage were conducted on silver foxes between 14 and 28 weeks of age; blue foxes were tested between 12 and 26 weeks of age. Experimental cubs showed significantly reduced fear responses to humans, suggesting that visual exposure led to habituation to events outside the cage. However, this experiment did not examine responses to other novel stimuli, thus failing to indicate whether habituation was specific to humans, or was generalised to any other events that might occur during management procedures. Visual exposure and handling may help cubs to become less fearful but the relative effects of visual exposure and of handling are not known. Absence of an opaque shelter within which the fox can hide forces the animal to have more visual contact with humans. A study of blue fox cubs by Bertelsen (1996, reviewed by Pedersen 1998) showed that those with no such shelter from 10 weeks of age were more fearful than those with a shelter in one test but not significantly different in another. Because the foxes are frightened by humans and often use the shelter when humans approach, their welfare is improved by the presence of the shelter on most occasions. Reduced adaptation to human presence, as a result of the possibility to hide, will result in poorer welfare when exposure to humans without a shelter is forced. However, forced exposure is much less common than the frequent exposure to humans during feeding and other farm work when a shelter could be used. Thus, the net effect of a well-designed nest box or other shelter is an improvement in welfare.

Interpretation of handling studies

Altogether, these studies make a strong case that early handling of cubs has beneficial effects on their welfare. The work of Pedersen (1994) indicates that early handling can have longlasting positive effects on captive fox welfare. In this case, the treatment tested was handling for three weeks post-weaning; however, work reported in Pedersen (1992) suggested that handling during weaning may have similar effects. Furthermore, 'forced' handling had stronger effects than 'gentle' handling, although it is important to emphasise that 'forced' refers to a specific mode of handling and should not be taken to mean 'rough' handling. Forced handling also involved transportation to a new cage, hence early experience of a new environment. Tennessen's (1988) experiment found more positive effects from five minutes of contact, and movement to a new cage, than from being picked up briefly. Gentle handling did not involve picking up or moving the cub, and may have had a different result if food had not been offered. For example, Bakken (1994a, b) reported results suggesting that the act of offering food items in itself may have effects on foxes. He visited one group of pregnant vixens twice a week and offered them food scraps by hand; another group received the same amount of human contact, but no food. Significant differences existed between the female cubs born to the two groups, with the females in the first group being more active and less fearful at 30 days of age than those from the second group. Bakken suggested that the act of offering food items was more effective than human contact alone in reducing the fear of humans in vixens, and that this affected the behavioural development of cubs. In another experiment (Bakken et al 1993), silver fox vixens that had learned to associate delivery of food scraps with a particular person showed sudden, strong behavioural and physiological responses when that person captured and handled them. Hence, as suggested by Pedersen (1994), gently handled foxes may have reacted more strongly to later handling not involving

food than those foxes that had never learned to make an association between handling and feeding.

In all, it seems that it is still not possible to precisely define the single most beneficial handling and human contact regime for fox cubs. For example, what is the age range within which handling has the most beneficial effect? Such information could help to encourage appropriate practices amongst fox breeders. Nonetheless, there is sufficient evidence that early handling and contact with the farm environment will benefit both foxes and farmers. Breeders should be encouraged to provide daily handling in the three-week period following weaning, if possible, involving brief transportation to another cage.

Bakken *et al* (1994) also noted that contact between foxes and caretakers seems to be important. They concluded that daily inspection, coupled with offering a biscuit, quickly reduced fear of humans, and improved reproduction in multiparous vixens. It may well be true that habituation to the presence of a human outside the cage is enhanced by maintaining daily contact, and that further benefits accrue. On the other hand, Braastad *et al* (1997, 1998) emphasised that not every kind of human contact is of benefit to animals: when pregnant blue fox vixens were handled for one minute daily during the last third of their gestation period, their offspring showed signs of significant negative effects. Careful research on human–farm fox interaction must ensure that handling and treatment procedures can be described in sufficient detail so as to rule out the possibility of misinterpretation during practice.

Physical aspects of the cage: size, materials and placement

Fox farms have come under public criticism for the small size of cages and the use of wire mesh for floors, which would appear to be uncomfortable to walk upon. Small variations in cage size with no enrichment do not have much effect on fox behaviour or physiology (Pedersen & Jeppesen 1998). Korhonen et al (1999) reported initial results from experiments designed to examine how farm foxes would choose between cage sizes and floor types. Blue foxes (16 adult, eight juvenile), initially housed in a standard mesh cage $(0.8 \times 1.05 \text{ m floor})$ area), were transferred to cages of 1.2 x 1.05 m, then cages of 2.4 x 1.05 m, then finally given access to an earthen-floor enclosure (1.2 x 1.05 m) immediately below the cage. Each of these conditions prevailed for two weeks. Foxes showed no change in activity as cage size increased and few foxes showed a tendency towards digging. Similarly, blue foxes housed in groups of two to six in large earthen-floor enclosures did not make even use of the available space, but tended to prefer certain areas for unidentified reasons (Korhonen et al 1991); results reported by Alasuutari and Korhonen (1992) in relation to eight foxes housed in one large enclosure (surface area of 224 m²) reveal the same tendency. Bakken et al (1994) reported as yet unpublished work by Korhonen in which farm foxes showed no clear preference when given the choice between conventional cages or 8 m^2 enclosures on the ground; in another experiment, the only change in behaviour seen when single foxes were housed in cages varying between 1-8 m² of floor size was that those in larger cages displayed more active escape behaviour, which declined over time in silver foxes but not in blue foxes.

The evidence regarding increased cage size is difficult to assess. Wild foxes do not use all areas of their home range equally, and may benefit from large enclosures such as those described by Alasuutari and Korhonen (1992) to a greater extent than has yet been measured. Nonetheless, behavioural evidence does not suggest that an increase in cage size of the order of 700 per cent is a valuable resource to farm foxes. Yet, resources and opportunities for complex behaviour are likely to be more important than space alone. Furthermore, research to date has examined cage size use and preference in adult farm foxes with no early

experience of different cage sizes: cubs exposed to larger areas for play and exercise could be expected to make use of these facilities as adults. Merely increasing cage size, without simultaneously increasing the complexity of the environment, may be of no benefit to farm foxes reared without such facilities. The provision of additional space is beneficial to foxes if it allows more cage enrichment which fulfils the animals' needs.

With regard to floor type, as examined by Korhonen *et al* (1999), results are inconclusive. Given large variations in earthen-floor usage amongst a small sample, and the potential effects of a fixed order of treatment on behaviour, further large-scale investigation might provide different results. Jeppesen and Pedersen (1990) and Skovgaard *et al* (1998) found that foxes raised on wire floors showed no preference for solid floors. A raised wire floor was preferred to an earthen floor (Korhonen *et al* 1999). However, it could be that early experience on wire, or with two floor types, is very influential. Bakken *et al* (1994) suggest that the cage system should be equipped with a portion with a solid bottom or finely meshed wire when cubs are small, because young cubs with poor co-ordination avoid walking on large-meshed wire floors.

Harri *et al* (1995b) noted that one experiment (Korhonen & Niemelä 1997) had unexpectedly shown that both silver and blue foxes spent more time in a high-mounted wire mesh cage than in an earthen-floor enclosure that was four times as large. These results, they reasoned, reflected the fact that silver foxes like to be in a high position with respect to their surroundings. They tested silver foxes' preference for floor level against their preference for floor type with the use of two standard cages, joined through contiguous holes, one of which had a wire floor and the other of which had a floor covered in a sand and peat mixture. Both cages had food and water and the experiment was divided into four two-week periods, during which: i) both floors were at ground level; ii) the wire floor was raised 50 cm higher; iii) the sand and peat floor was raised 50 cm higher (and the wire floor returned to ground level); iv) both floors were raised to the height of 50 cm.

In this study, foxes showed a preference for the sand and peat floor for both rest and activity. This was most noticeable at the beginning of the experiment, when both floors were at the same (ground) level. Use of the cage with the wire mesh floor as a resting area increased when it was raised 50 cm higher, and its use during resting remained at about the same level when it was subsequently lowered and raised. This suggests that the wire floor had some value as a resting place, possibly because of the exceptionally hot weather which the authors reported accompanied the experiment. However, regardless of the position of the wire floor cage, the other cage was used more for activity and as much or more for resting. The authors also commented that in the study by Korhonen and Niemelä (1997) that found equal distribution of activity between a wire-bottom and a solid-bottom cage (see also Bakken *et al* 1994), a long tunnel rather than a single hole was used to connect the cages; thus, it is possible that the apparently equal distribution of activity reflected a preference to travel through the tunnel, rather than a preference for floor type. Whether or not this is what occurred, such a suggestion highlights the importance of identifying extraneous variables that may erroneously create or hide an effect.

Results obtained by Harri *et al* (1995b) therefore suggest that adult silver foxes show a preference for a solid floor, at least when that floor is higher than, at the same level as, or no less than 50 cm below, a wire floor. The wire floor section of the modified cage, however, was used in 97 per cent of defecations, suggesting that foxes in cages equipped with a portion of each type of flooring may quickly learn to defecate over the wire, thus ensuring cage hygiene.

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Two inconclusive studies have been carried out in an attempt to examine the implications of the physical placement of cages on a fox farm. Kaleta and Stosznajder (1990) reported that in response to a human approaching rapidly, foxes housed in cages placed in the standard 'pavilion' sheds showed withdrawal and immobilisation, whereas foxes in freestanding cages showed a greater tendency to try to escape. The result was that foxes in pavilion cages allowed human observers to approach more closely, but this result did not demonstrate that foxes showed less fear under either condition. The authors concluded that the presence of farm workers was more disturbing for animals in pavilions, although it is not possible to judge whether this conclusion is justified. In another paper, Kaleta and Plochocka (1990) studied 534 two-month-old silver foxes of both sexes, housed in pairs in free-standing cages. They looked at the relationship between aisle width and the distance at which the foxes first moved away from an approaching human ('escape distance'). Foxes were approached perpendicularly, presumably as an attempt to control for the effects of the differing widths of aisles. Results showed a positive correlation between aisle width and escape distance: for example, when the aisle width was 1.4 m, escape distance was 1.03 m; when aisle width was 3.9 m, escape distance was 2.0 m. This result seems to have little relevance: when the aisle is a few metres wider, the fox reacts to an observer who is further away. This is unsurprising because a person three metres away in an aisle 1.4 m wide may not be as visible to a fox as a person three metres away in an aisle 4 m wide. This experiment justifies no real conclusion with regard to the differential welfare implications of the width of aisles.

Enrichment of the barren cage environment

Efforts to provide environmental enrichment for farmed foxes have focused on the provision of nest boxes outside the breeding period, and on observation or resting platforms. Extensive studies have examined use and preferences of both species under a variety of conditions.

There is good evidence that additional shelters, whether platforms or nest boxes, are not necessary for adult foxes to protect themselves from cold weather. Experiments on animal models found that fur provides a six-fold reduction in heat loss: with fur, heat loss is only 10 per cent less inside a nest box than lying outside on wire mesh (Harri *et al* 1989). Further experiments have shown that the saving in heat loss when a fox model was stretched out across a wooden platform was so low as to be of no practical use to the animal (Bakken *et al* 1994), and Scholander *et al* (1950) estimated that an Arctic fox does not have to increase its basal metabolic rate until the temperature falls below -40° C. Observations have shown that the use of platforms and nest boxes in both species decreases with decreasing temperature, and that use drops in winter (Harri *et al* 1988, 1991, 1992; Korhonen *et al* 1991; Mononen *et al* 1993; Korhonen & Niemelä 1996c; Korhonen *et al* 1996).

Nest box for foxes

Some studies indicate that year-round provision of a nest box can significantly improve welfare. In a two-year study of 100 silver fox vixens, Jeppesen and Pedersen (1991) found that animals in cages provided with such nest boxes spent 5–25 per cent of their time inside it under quiet conditions. When disturbed, those with nest boxes either hid in them or moved closer to them, whereas control foxes moved to the back of the cage. At the end of the study, foxes that had been housed with nest boxes had lower base levels of cortisol and eosinophils, and higher base levels of lymphocytes, suggesting lower stress levels than those of control animals. They responded less fearfully to humans outside the cage, and showed more activity and exploration in an open field test. The possibility that escape to a nest box may have

provided foxes with some degree of control over their interactions with the outside world is supported by the authors' observations that the control animals acted as if they were in an uncontrollable stressful situation.

The extent to which foxes use year-round nest boxes has been the subject of considerable debate as figures for mean usage vary between individuals and between studies. Harri et al (1992) provided pairs of weaned silver foxes with nest boxes on the floor of the cage. They found that foxes spent very little time in them, but spent a major part of their daily time on the roof of the nest box. Mononen et al (1995b), in a study of 36 pairs and eight singly housed juvenile silver foxes that had been provided with floor-level nest boxes, also found them to spend only one to two per cent of their time inside nest boxes, but more than 50 per cent (over a 24 hour period) on the roofs of nest boxes. These authors supposed that this behaviour might result from the fact that placement of the nest box took up part of the floor space and restricted the view of the surroundings. Mononen et al (1996a) made a further assessment of the preferences of both silver and blue foxes for cages containing floor-level nest boxes, using a set-up in which one cage, provided with a nest box, was joined via an opening to a standard, empty cage. They found that both species spent more time in the cage containing the nest box, although not necessarily in the nest box itself, and that only silver foxes showed a strong preference for the roof of the nest box as a resting site (44% of daily time was spent there). In the wild, foxes may rest within the vicinity of a den without actually entering (Weber 1985); thus, as has also been concluded by Bakken et al (1994), it is not necessarily the case that dens (or nest boxes) are not important to foxes that do not make high use of them.

The height at which a nest box is placed may have additional welfare implications. Pedersen and Jeppesen (1990) found that silver foxes spent 80 per cent of their time at night inside nest boxes that were mounted on the roof of the cage and accessible via a platform. Similarly, vixens preferred a nest box under the roof to a box on the floor (Jeppesen & Pedersen 1990). In a study conducted during farm working hours only, Pedersen and Jeppesen (1993) observed silver and blue foxes in complex cages that featured access to an open-topped floor-level box, an adjoining closed nest box, and a nest box mounted on top of the cage with a platform beneath. Both fox species used the nest boxes to varying degrees over the study period: for example, use increased just before the breeding season, as is true of den use amongst wild foxes (Macdonald 1980). Silver foxes used all types of constructions frequently at the beginning of each observation period, suggesting that a high level of activity throughout the nest box system was provoked by the renewed presence of the observer walking past the cages. When actively disturbed by a person hitting the cage with a stick, silver foxes fled to the opposite side of the cage, or into the top box; most of the blue foxes fled into the top box. Both species of foxes preferred the top box and the shelf beneath: silver foxes spent most time on the shelf, blue foxes spent most time in the top box. This study clearly shows that nest boxes were more attractive to both species when they were mounted above the cage.

The experimental set-up used in this study involved two standard cages with an access hole between them, a ladder against either side of the adjoining hole, and the nest box additions to one side of the cage: thus, in effect, housing conditions were both enriched and enlarged. Foxes used in experiments might have been shown to benefit from this if they had been compared with controls in standard cages. Nonetheless, no direct measurement was made of the effects of increased size in conjunction with a more complex environment.

Another aspect of this study is that all individuals used all of the space available during active behaviours. While the experiments reported above (eg Korhonen et al 1991) showed

that foxes used only small areas of large barren enclosures, this cage system was both enlarged and more complicated, involving climbing ladders and jumping onto the nest box. Harri *et al* (1995a) reported that when standard-sized cages were joined by a simple opening, silver foxes changed sides up to 250 times a day, but when cages were connected with a long (1.5 m) tunnel, the number of cage exchanges ranged as high as 500 times per hour. These observations suggest that foxes respond with increased activity to increases in the complexity of the standard barren cage.

With regard to the nest box itself, a few studies have examined design issues. Although farmed adult foxes do not need additional thermal protection from the environment, fox cubs in their first few weeks of life are vulnerable to hypothermia. However, extra insulation of the nest box makes little difference to cubs' rate of heat loss (Bakken *et al* 1994); neither does the extent of ventilation provided in commercially available nest boxes make a significant difference to the thermal environment, even under windy conditions (Harri *et al* 1989). As the most important source of heat to cubs is the vixen, Bakken *et al* (1994) recommended that cubs will have the best chance of survival through the selection of foxes for good maternal care.

However, Braastad (1990a) reported that when the nest box was equipped with a narrow entrance tunnel, a smaller proportion of vixens committed infanticide, and average litter size at weaning was 0.5 cubs higher than in foxes with standard breeding boxes. In a study of 834 silver fox vixens on nine farms, Braastad (1994) found that vixens provided with a nest box that included an entrance tunnel (20 cm long x 18 cm wide; see Braastad 1994, Figure 1) bore more offspring and had lower cub mortality up to three weeks after birth. The effect was more pronounced in primiparous vixens, which are often less successful, and was not seen at all at two farms that had high reproductive success, thus suggesting that such a design can improve sub-optimal breeding success. Behavioural observations indicated that vixens were calmer and did not show increased activity during working hours as is typical for vixens in traditional boxes (Braastad 1992, 1994). It would seem that this improvement to the traditional next box benefits silver foxes both in terms of their welfare and their reproductive success.

Observation platforms and an unobstructed view

Early work in which foxes were provided with platforms 20–30 cm from the cage roof suggested that they were used to view the surroundings, much as has been reported for Arctic foxes in the wild (Chesemore 1986; Korhonen *et al* 1991). Seventeen of 18 blue foxes provided with wooden or wire shelves preferred to sleep on the wire cage floor; however, all animals used the shelves to different extents (Harri *et al* 1988). Shelves were generally used for short bursts of activity only, and generally during farm working hours, particularly as animals awaited feeding. Harri *et al* (1991) found that all 47 experimental blue foxes used platforms, on average, for 6.8 per cent of their daily time, although some individuals lay on a platform for hours. Korhonen *et al* (1991), studying blue foxes in enclosures of various sizes, also found that foxes preferred to sleep on the cage floor, but that those provided with shelves used them as a vantage point. Harri *et al* (1992) found that silver foxes preferred platforms from which they could observe the shed house door to platforms facing in the opposite direction (P < 0.001). They also reported that any 'extraneous' disturbances on the farm led foxes to use platforms. Korhonen and Niemelä (1996c) reported that silver fox use of platforms was high, with the greatest use made between 0400h and 0500h.

The evidence indicates that foxes make greater use of platforms that do not have walls. Harri et al (1991) found a highly significant difference in blue fox usage of platforms with

and without walls. Korhonen and Niemelä (1996a) compared the use of walled and open platforms in two groups of 30 foxes each. They found that in both sexes, foxes made significantly greater use of open platforms. They were used for jumping, resting and sleeping upon. A disturbance test, in which an experimenter struck the cage with a stick, indicated that most foxes jumped onto open platforms (62.5% of males and 85.7% of females), but significantly less use was made of walled platforms. The authors concluded that foxes avoided walled platforms because they prevented observation of the surroundings. The likelihood that the opportunity to observe surroundings is important to foxes has been further supported by Mononen *et al* (1995a, 1996b). They housed a small number of adult silver and blue foxes (four of each) in double cages and used wooden boards to alternately obstruct the view that was available from a lying position in each cage. Both species spent a lesser proportion of their time in the cage with an obstructed view, and almost exclusively preferred the cage with an unobstructed view as a resting place. The authors concluded that an unobstructed view is a key feature of housing design.

This poses the question of exactly what the foxes are viewing. Evidence from Rekilä et al (1994, 1996) suggested that adult farmed foxes are affected by the environment outside the cage. They found that foxes from cages in the front half of the rows in sheds appeared better adjusted to the farm environment than those in cages at the rear. Foxes in the former group were more active, both in the home cage and in an open field test, and the majority were sufficiently confident to eat in the presence of a human outside the cage (this was not true of foxes from rear cages). It seems likely, as the authors suggested, that this difference arose because foxes near the front of the barn were more frequently exposed to humans and regular farm activities, and thus became habituated, or were better adjusted because of higher levels of sensory stimulation. An unexplained finding in a study of platform use by Korhonen and Niemelä (1994b) — that the location within the cage of the platforms affected their usage might be explained by factors present in the external environment, such as the proportion of other foxes that have platforms, the social relationships between neighbours, and the extent and nature of activities that occur in the vicinity. Factors in the external environment may also explain the often-remarked high degree of inter-individual and inter-study variation in platform use (see Bakken et al 1994).

The extent of platform use varies seasonally. Korhonen and Niemelä (1994b) suggested that platform use by blue foxes during winter was so low as to render them unnecessary at this time: only 5–15 per cent of animals used platforms at all during mid-winter. However, Korhonen *et al* (1996) and Korhonen and Niemelä (1996c) agreed that platforms could be recommended for both fox species, particularly during spring and summer. Studying male and female blue foxes throughout the year, Korhonen *et al* (1996) found that platform use by all experimental animals was highest from August to October. Lactating vixens tended to lie on the nest box roof rather than the platform, but males and non-breeding vixens showed high platform usage during the whelping season, with platforms predominantly used for sleep. In a study of 120 silver foxes and 300 blue foxes, Korhonen and Niemelä (1994c) also reported that platforms were used predominantly for sleeping, thus it is clear that the utility of platforms is not restricted to their use as a vantage point during short visits.

In terms of production parameters, no differences between weight gain or reproductive performance were found in a comparison of blue foxes housed with and without platforms (Korhonen & Niemelä 1994a). Wire mesh platforms remained cleaner, and fur quality was worse on dirty platforms. As blue foxes used wire and wooden platforms equally, the authors concluded that a wire mesh platform was probably preferable from the farmers' point of view.

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In terms of general fearfulness, Korhonen and Niemelä (1996d) administered several behavioural tests to silver foxes housed in groups with and without platforms. Altogether, there was no difference in fear of non-human stimuli between the two groups, although those housed with platforms were significantly less fearful of humans. While Rekilä *et al* (1996) reported that blue foxes housed either with year-round nest boxes or with platforms were no less fearful of humans than control foxes, one can at least conclude that these modifications to the environment did not cause blue foxes to be more fearful of humans because of reduced contact.

Although reproductive success may not be improved and fearfulness of humans may not always be reduced, and despite seasonal, individual and species variations in platform use, it is clear that the addition of platforms to cages provides environmental enrichment. These studies have shown that platforms have been used by foxes of both species for a range of biologically appropriate behaviours, and they evidently can increase the complexity of the environment for foxes. Furthermore, it seems that the available view of the surroundings and of the events that occur outside of the cage environment should be considered as aspects of housing design. In some countries, platforms must be provided in fox cages. The evidence suggests that simultaneously increasing the cage size and complexity will have a positive effect on farmed foxes.

The social environment: group housing and effects on reproduction and welfare

The possibility of housing farmed foxes in enriched or semi-natural enclosures in social groups has also been examined. Korhonen and Niemelä (1996b) devised a complex, enriched environment involving several tunnels, two earthen-floor enclosures, top-mounted and floor-level nest boxes, and a variety of platforms. Here, they housed 16 male and 14 female juvenile blue foxes. These animals were handled by three different handlers for a period of 10 minutes, five days a week, for an unknown period. A few months later, they were compared, in terms of behaviour and production parameters, with cubs housed singly in standard barren cages from the same litter. These foxes had not been handled.

Some positive aspects arose from the complex housing, indicating an enriching effect on foxes. The housing provided appropriate opportunities for foxes to rest, observe their surroundings, retreat from each other, interact, bite and dig. The authors conducted an evaluation of fear in relation to humans by putting each experimental fox into a single cage, then opening the door and scoring the reaction to a person reaching inside. They concluded, on the basis of their results, that handling had a positive effect on foxes' reactions to humans, although this is not truly evident from the results given that the only reported difference is that four more animals from the handled group were assessed as being curious rather than fearful. Handling was not conducted in the manner that has been proven to have long lasting effects on fox cubs (see above): it occurred later than the optimal period, and may not have involved all cubs, for the handler only touched those that approached him or her. It is not clear whether the same conditions prevailed for experimental and control animals during the fear test — in other words, whether control animals were placed into new cages prior to testing or whether they were housed in their home cage. If the latter is true, the lack of difference between experimental and control animals might be taken to indicate greater confidence in new environments amongst experimental animals. This, therefore, might be the effect of physical or social enrichment, as well as handling.

However, negative effects of social interaction arose. Although more feed had to be given to experimental animals (amounting to 50 g fox⁻¹ day⁻¹) to ensure that all were able to feed, experimental females were significantly lighter than control females (there was no difference

between the groups of males). Strongly manifested dominance relations prevented lowerranking animals, often females, from feeding as much as higher-ranking foxes, as was also reported in the group-housing experiments of Korhonen and Alasuutari (1994, 1995). Fur quality was poor amongst all group-housed foxes, at least partly because of biting, but no control group foxes had poor-quality fur. Reproductive behaviour showed some parallels with behaviour in the wild: following whelping, females moved cubs between different nest boxes almost daily, and occasionally a non-breeding female assisted with the cubs. However, only two females had litters, and only three cubs from one of those litters survived. The average number of surviving cubs amongst control females was 7.9. As Korhonen and Niemelä (1996b) conclude, these effects on body size, fur quality and reproduction would not seem to render group housing of this type a practical option for farmers.

On the whole, group-housing experiments have shown poor reproductive success (Kullberg & Angerbjörn 1992; Korhonen & Alasuutari 1991, 1992, 1994, 1995). Yet, the authors recognise that their attempts at social enrichment have not been optimal: social groups that occur in the wild involve closely related animals only, and this has not been true of most of these experiments. In the one situation in which one male blue fox was housed with three female sisters, two successfully raised litters and the female who lost her litter helped in raising another's cubs. In this same group, the father remained close to one of the successful mothers, stayed with the cubs and brought food to the mother.

Bakken *et al* (1994) described unidentified Danish studies of both silver and blue foxes in which animals were kept singly or in groups of two, four and eight foxes at a constant density ratio of one fox per square metre. It is not known how many control animals were involved. These studies were said to find that, amongst silver foxes, those housed in groups had a higher growth rate and more activity than controls and, apart from a few biting injuries, there was no significant difference in fur quality or fur damage. Amongst blue foxes, activity levels were highest amongst group-housed animals, and there was no difference in growth rate and fur quality.

Bakken et al (1994) suggested that problems arising from group housing systems are mainly restricted to the breeding season; in most published studies, insufficient information prevents the assessment of this possibility. Certainly, group-housed animals have been reported to make attempts to escape as the breeding season approaches (Korhonen & Alasuutari 1994; Korhonen et al 1997). Perhaps, if foxes were housed in small groups of closely related individuals in enlarged, complex environments (such as that in Korhonen and Niemelä [1996b]) outside the breeding season, then moved to normal breeding conditions, the suggested positive effects of social and physical enrichment would be seen without the negative effects on fur quality and reproductive success.

Reproduction issues: maternal infanticide, the influence of neighbours and further abnormal behaviour in captivity

Killing and injury of cubs is a common problem on fur farms (Braastad 1990a,b; Bakken 1998). A survey of all fox farms in Germany found that 45 per cent of silver foxes and 40 per cent of blue foxes failed to breed (Haferbeck 1988, and personal communication 1994): this figure is substantially higher than the average of 20.5 per cent in the wild (see Lloyd 1980b). However, reports from fur farming organisations, although unverifiable, suggest that Haferbeck's figures are much higher than the norm for fox farms. Whereas much reproductive failure in the wild is attributable to lack of food, farmed foxes are generally well fed. Reproductive failure, when there is adequate opportunity to reproduce, is an indicator of poor welfare (Broom & Johnson 1993).

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Wiepkema (1994) estimated that 10–20 per cent of female farm foxes show infanticide at some time, but the data upon which this estimate is based are not presented. This is obviously a substantial welfare problem. Amongst farmers, cub killing has often been thought to arise from stress caused by the farm environment, or vixens with pathological social behaviour (Bakken 1993a,b). However, research now indicates that some vixens may kill and injure their own cubs because of the neighbours alongside which they are housed. In either case, poor welfare of the vixens is indicated and the welfare of the killed cubs may be very poor before death.

Braastad (1988) showed a relationship between fearful behaviour and poor reproduction. Braastad and Bakken (1993) studied the behaviour of 21 primiparous and 18 multiparous vixens. Of 54 dead cubs, 41 had been bitten and probably killed by their mother. Seventeen vixens were categorised as infanticidal. Half of these bit off the tails of their cubs prior to killing them. Quantitative analysis of behaviour in relation to cubs showed that both infanticidal and non-infanticidal vixens exhibited similar behaviour, including the same amount of cub grooming: the only observable difference was that infanticidal vixens stood during grooming and appeared more restless in the nest box. Infanticide, therefore, did not appear to be the result of inept breeding behaviour. Neither did it appear that particular disturbances on the farm initiated cub killing. However, cub killing was restricted to certain individuals, with infanticidal vixens repeating their behaviour in later years. Moe (1996) reported that infanticidal vixens showed the most pronounced stress-induced hyperthermia response, a response that is readily induced by human proximity.

Studies have shown that infanticidal vixens, or those with lower reproductive success, tend to have lower social status than successfully reproducing vixens (Bakken 1989, 1992, 1993b). In the wild, reproduction is often suppressed in subordinate foxes. Braastad and Bakken (1993) therefore suggested that infanticidal behaviour may be the result of lowsocial-status vixens choosing not to reproduce in a given year, only to find that they cannot change their strategy in subsequent years because the social housing conditions on the farm remain static. The suggestion that infanticidal vixens are affected by the presence of their neighbours was borne out in the work of Bakken (1993b) in which 16 vixens that had been infanticidal were physically and visually isolated from other vixens. They then raised significantly more unharmed cubs. Furthermore, Bakken (1993a) kept vixens with more dominant or subordinate neighbours and studied the consequences for the cubs. He found significant variation in infanticidal behaviour according to the social status of vixens' neighbours. There were no significant differences according to the degree of dominance or subordination, or to the kind of neighbour, in the number of cubs born, and even isolated vixens lost half of their cubs. However, vixens of low competitive ability killed or injured more cubs than those of high competitive ability. Altogether, of 153 cubs born, 77 were killed or injured by their mothers. Dead cubs had bite marks on their bodies, often had the skull crushed, and were sometimes half-eaten. Bakken found that vixens of high competitive ability with neighbours of low competitive ability weaned the most unharmed cubs. No vixen of low competitive ability weaned unharmed cubs if she had neighbours of high competitive ability; however, such vixens did wean unharmed cubs when they had neighbours of low competitive ability. Pedersen (1998) studied reproduction and behaviour in silver fox vixens kept together and found a high occurrence of infanticide, most often by the subordinate vixen. The two vixens sometimes both produced cubs but there was also more frequent failure to reproduce, the exact mechanism being unclear.

These studies raise two important issues. Firstly, it is clear that the physical placement of the cage within the housing system can have a highly significant effect on welfare. Given the

demonstrated effects of status-linked infanticide, and the fact that a vixen's status is rarely known to their human keepers, it seems highly likely that a proportion of low-status vixens under standard farm conditions will always have poor welfare and kill or mutilate their own cubs. Secondly, cub mortality because of infanticide exceeded 50 per cent in the study by Bakken (1993a). Braastad and Bakken (1993) reported that the probability that a cub with a primiparous mother would be killed was 0.37. These figures seem extremely high, and yet no papers other than those reviewed in this section mention the incidence of infanticidal behaviour. Indeed, although it is reported that reproductive success varies between and within standard farming systems, nor what the average rate of infanticide is on farms beyond the limited information given here. Accurate data are difficult to obtain on commercial farms because dead pups are usually eaten, whatever the cause of death.

In terms of other abnormal behaviours, almost no mention is made in the literature of stereotyped behaviour, with the exception of Jeselnik and Brisbin (1980) in relation to two captive foxes, and remarks by Braastad (1992, 1993). Braastad (1993) commented that in a study of silver fox vixens, all animals persistently performed digging movements on the wooden floor of the breeding box prior to delivery. During the last pre-parturient day, vixens 'excavated' for a total of 102 minutes, in long bouts of several minutes. Some silver fox vixens also performed stereotyped digging that may have been motivated by hunger. Braastad (1992) commented that stereotypies in foxes have not been systematically studied. Thus, it appears that the extent of abnormal behaviours such as infanticide and stereotypies, which indicate poor welfare, is not sufficiently documented in relation to fox farms.

Whether cubs, which, in the wild, often remain in their natal territory until at least six months of age, would benefit from being left with the vixen for a longer period is unknown. The effects of olfactory or auditory stimuli from conspecifics are unknown, but it seems likely that animals with advanced usage of such senses will be affected in ways that are not easy for humans to appreciate.

Conclusions and animal welfare implications

i) Extensive studies of wild foxes reveal that they are complex animals. They spend a long time (up to six months) rearing their cubs, they travel long distances, and red foxes make patterned use of large home ranges. Social behaviour is varied, and social status strongly affects group relations and productivity. Males and non-breeding vixens play a role in rearing the cubs. Reproduction is evidently controlled by complex factors. Foxes seek cover regularly and may use several dens. Those wary of conspecifics may attempt to avoid leaving scent trails, and the relative importance of scent-marking of paths and caches via urine or gland secretions cannot be assessed. Foxes are probably capable of a high degree of learning, and show evidence of lasting memory and, possibly, use of cognitive maps. On fox farms they are almost always kept in small, barren, contiguous cages with no physical enrichment other than a wooden nest box when whelping and sometimes a wire mesh platform. They live in a largely static social environment, determined haphazardly. They have no opportunity to adjust their distance or take shelter in relation to aversive stimuli such as the presence of conspecifics or humans. The effects of sensory variables, such as olfactory and auditory cues, on foxes housed in large numbers in farm sheds are unknown.

ii) Research on fox welfare in relation to housing shows that farmed foxes have a considerable degree of fear, both of humans and in general, that the barrenness of cages is a significant problem for the foxes, and that farmed foxes can have substantial reproduction

problems. There is clear evidence that the welfare of farmed foxes in the typical bare, wiremesh cages is very poor.

iii) A long-term selective breeding experiment on silver foxes in Siberia appears to have successfully produced foxes that are less fearful under farm conditions. Some comparable experimental results have been obtained in Europe, but the programme is long-term and significant results are not yet available.

iv) Studies of early handling of fox cubs make a strong case that this treatment can have a beneficial effect on long-term welfare in terms of reducing fearfulness. Handling twice daily for three weeks post-weaning, involving firm handling (in contrast to fondling) and brief removal into another cage, has a long-lasting effect on fear responses to a human reaching for the fox, and to novel objects. Research suggests that non-handled foxes are chronically stressed. Given that foxes on farms are frequently removed from their cages by humans, fear of humans is a significant welfare problem. Treatments that can reduce such fear are to be recommended, but it is questionable whether farmers will give the time required for such treatments.

v) Increases in the size of the barren cage, without a consequent increase in the complexity of the environment, do not appear to benefit farmed foxes. However, larger space allowances for foxes can make real enrichment possible.

vi) Some studies have shown that year-round use of a nest box can have significant benefits for farmed foxes; others indicate that they are not used often by foxes. Nest boxes are likely to enrich the environment even if they are seldom used. It is clear that the addition of viewing platforms to cages provides environmental enrichment for the majority of foxes. Platforms of appropriate size have been used by captive foxes of both species for biologically appropriate behaviours, and they can evidently increase the complexity of the environment for foxes. Nonetheless, insufficient attempts have been made to add further physical enrichment and complexity to the cage system of singly housed foxes.

vii) It seems likely that the opportunity to view the surroundings is an important aspect of captive fox housing. Experience obtained from outside the cage, including that resulting from humans and other foxes, has been shown to affect foxes. It may well be the case that daily activities and various seemingly innocuous events have an unnoticed effect on captive foxes. Traditional fox cages are up to one metre high and any shelf is therefore unlikely to be high enough to provide an adequate viewpoint. Much more elaborate cages, or systems of linked cages rather than simple cages, would be much more likely to provide for the needs of foxes.

viii) The traditional wooden nest box, provided for vixens during the breeding season, can probably be improved.

ix) Experiments involving group housing of animals in large enclosures or complex cage systems have shown some beneficial and some detrimental effects. It may be possible to overcome the detrimental effects if foxes are not group-housed during the breeding season. In such studies, insufficient account has been taken of the social problems likely to be inherent in housing unrelated foxes together.

x) The extent of stereotyped behaviour in farmed foxes is not adequately documented.

xi) The incidence of abnormal behaviours in farmed silver foxes is cause for serious concern. The killing and injury of cubs (tail removal, biting) by their mothers has been reported as a common problem on fox farms, and yet comparatively few studies have examined this issue. The extent of infanticide on farms is not known. Experiments have shown that visual isolation of low-status females and manipulation of the social status of neighbours can lead

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suggests that reproductive performance is inhibited and infanticidal behaviour enhanced among many low-status females on farms today.

xii) A combination of selective breeding, appropriate early handling and major changes in cages and management so as to provide for the needs of the foxes will significantly improve welfare. However, in the light of the cautionary comments made in conclusions iii), iv), vi), vii), ix) and xi), it is clear that the desirable major improvements in welfare will be difficult to achieve.

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